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A MONOGRAPH OF THE MONIMIACEAE (LAURALES) IN THE MALAGASY REGION (SOUTHWEST INDIAN OCEAN)[1,2,3]

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ABSTRACT

A systematic, ecological, and evolutionary study of the Monimiaceae of the islands in the Malagasy floristic region, southwest Indian Ocean (Madagascar and the Mascarene and Comore archipelagos), is presented. The Malagasy Monimiaceae are here taken to comprise four genera and 55 species, all endemic: *Monimia* (3 spp., Mascarenes); *Decarydendron* (3 spp., Madagascar); *Ephippiandra* (6 spp., Madagascar); *Tambourissa* (43 spp., Madagascar, Mascarenes, Comores). Madagascar, a large, ancient continental island, is the regional center of diversity with three genera and 35 species. The smaller, younger volcanic islands harbor fewer taxa: Mauritius (2/11); Réunion (2/5); Anjouan (1/2); Grand Comore (1/1); Mayotte (1/1); Mohéli (1/1); Rodrigues (0). Synopses of the family's taxonomic history, biogeography, and distribution are given. The regional setting is defined and summaries of the geology, geomorphology, and climate of each island given. Distribution of species according to habitat is discussed for each island and ecological observations are presented. Vegetative and floral morphology and anatomy are described from both the literature and original observations. A synopsis of the palynology is given. Cytological investigations of ten species of *Tambourissa* revealed all to have $n = 19$. Results were inconclusive for *Monimia* but suggest it is polyploid with $n =$ ca. 44–48. Field studies on floral biology of *Tambourissa* revealed that variations in floral morphology, color, and odor are responsible for several different pollination syndromes involving Coleoptera and Diptera. Breeding experiments demonstrated a strong tendency towards outcrossing via self-incompatibility in most monoecious species. Population density was related to pollinator systems in the three species studied.

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In the taxonomic treatment, keys to genera and species are provided. Synonymy, descriptions, distribution, habitat, discussions, vernacular names, economic uses, and herbarium specimens are given for each species. *Hedycaryopsis* Dang. is united with *Ephippiandra* Decne., thus necessitating the following new name and combinations: *E. domatiata* Lorence (basionym: *H. capuronii* Cav.); *E. madagascariensis* (Cav.) Lorence; *E. perrieri* (Cav.) Lorence. *Ephippiandra capuronii* Cav. is transferred to *Tambourissa* as *T. beanjadensis* Lorence. Finally, *Phanerogonocarpus* Cav. is united with *Tambourissa* Sonn. and the following new names are proposed: *T. alaticarpa* Lorence (basionym: *P. perrieri* Cav.); *T. longicarpa* Lorence (basionym: *P. capuronii* Cav.).

This monograph represents a systematic, ecological, and evolutionary study of the Old World Monimiaceae (Laurales) occurring in the Malagasy floristic region of the southwestern Indian Ocean, here taken to include the microcontinental island of Madagascar and its satellite islands, the Mascarene and Comore archipelagos (Figs. 1, 2). On many of these islands Monimiaceae constitute an important woody element of the wet and cloud forest formations.

Monimiaceae were chosen for study because they are a large and diverse but poorly known family belonging to the so-called "woody Ranales" that have played a key role in interpretation of the morphological and evolutionary patterns of primitive angiosperms. Extensive adaptive radiation into four genera and some 55 species, all endemic, in the islands of this region suggests that the Monimiaceae hold a unique position as a model for island evolution by a relict group of plants. Study of the family is all the more imperative in view of the threat posed by man's destructive activities in the region coupled with the relentless invasive competition from introduced plant species.

In spite of their importance as floristic components on many of these islands, the Monimiaceae have never been the subject of a detailed field study. Not only has there been a dearth of knowledge regarding their ecology and biology, but lack of field studies has also resulted in considerable taxonomic confusion because of the difficulty in matching androecious and gynoecious flowering material and of understanding morphologically variable species.

During the course of this work I was able to spend an entire year in the Malagasy region studying and collecting Monimiaceae in their native habitats in the following islands: Mauritius (where the majority of the work was carried out), Réunion, Madagascar, Mayotte, and Grande Comore. As a result, I have seen about half the species in the field and have accumulated a great deal of new ecological and biological information that is incorporated into this monograph.

TAXONOMIC HISTORY OF THE MONIMIACEAE

The Monimiaceae sensu lato are an old and diverse assemblage of about 30 genera and nearly 350 species widely distributed in the tropics and subtropics, especially in the southern hemisphere. The family has undergone a great deal of taxonomic flux because of the striking diversity of its members, which display various combinations of primitive and advanced characters.

Evolutionary advancement in floral morphology of the Monimiaceae is generally expressed in terms of reduction, both in size and number of parts; in rearrangement of their orientation from spiral to radial and finally to decussate; in closure of the female floral receptacle; and also in a transition from free stalked carpels to an inferior syncarpous gynoecium (Corner, 1976). Other advanced trends occur in wood anatomy, with simplification of the vessel members; in pollen; in leaf architecture; and in a progression from floral bisexuality to monoecy and finally dioecy. The Monimiaceae have a long and interesting taxonomic history dating back nearly two centuries.

De Jussieu first founded the family in 1809 (as Monimieae) based on three previously described genera: *Monimia* Thouars, *Atherosperma* Labill., and *Siparuna* Aubl. (as *Citrosma* Ruiz & Pav.). Tulasne subsequently monographed the family in 1855 (1855b), including seven additional genera and subdividing it into three tribes on the basis of characters of the fruiting receptacle. Baillon (1868–1870) circumscribed the family in a much broader sense to include the present day Calycanthaceae and Gomortegaceae, defining five series or tribes: Calycantheae, Hortonieae, Tambourisseae, Atherospermeae, and Gomortegeae. Bentham and Hooker (1883) recognized only two tribes (Monimieae and Atherospermeae) based on features of the anthers and ovules, adding more genera but excluding the Calycanthaceae. This system was also followed by Pax (1891), who raised both tribes to the subfamilial level (Monimioideae and Ath-

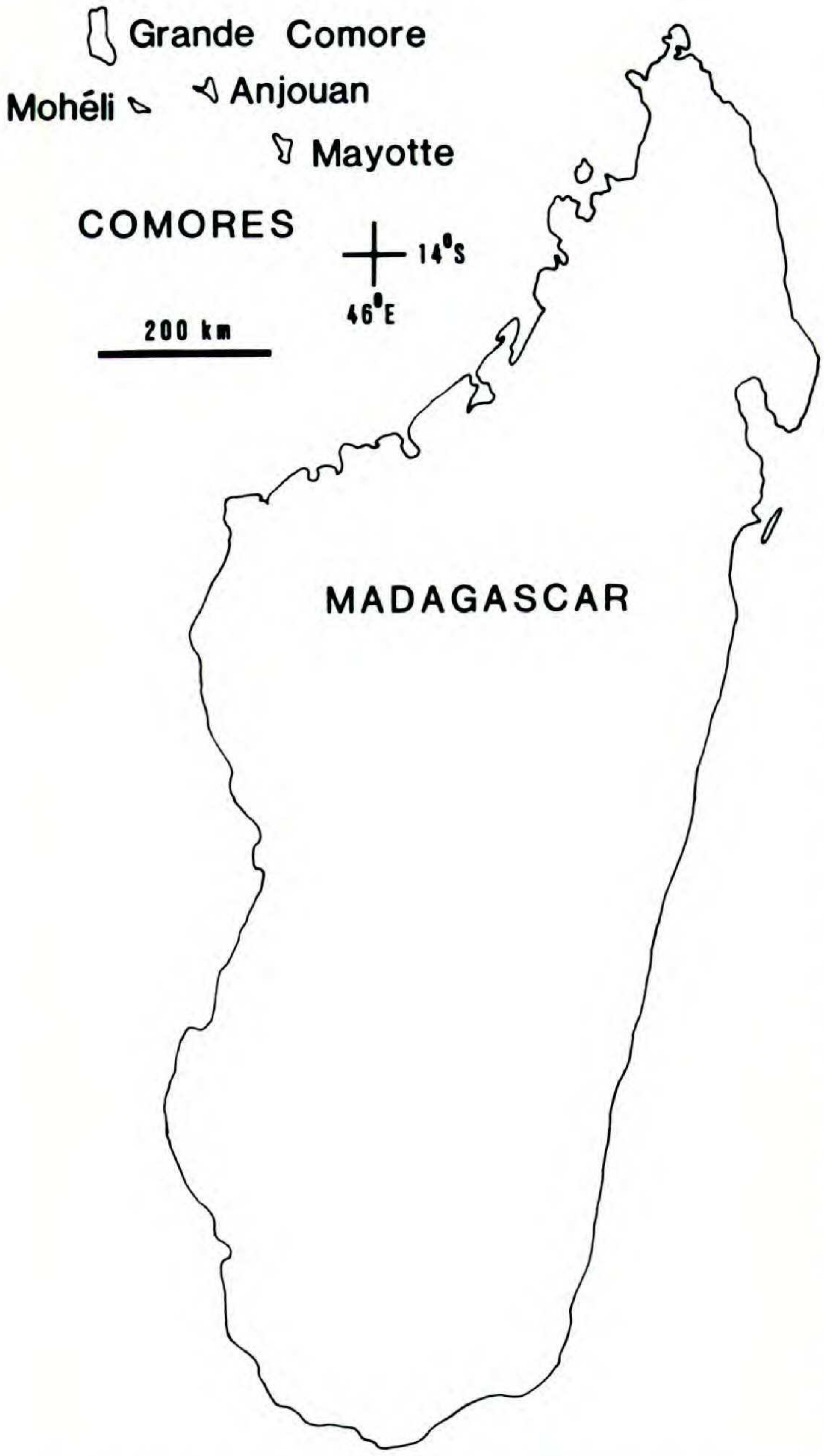


FIGURE 1. Regional map of study area, showing Madagascar and the Comore archipelago.

erospermoideae) and created six tribes for the species groups of Bentham and Hooker.

In their monograph of the family for "Das Pflanzenreich," Perkins and Gilg (1901) followed Pax, and Bentham and Hooker in recognizing two subfamilies but modified the tribes, creating an additional one under Monimioideae and merging two under Atherospermoideae. Perkins (1911) later updated the earlier revision using the same system. Hutchinson (1964) more or less followed Bentham and Hooker in dividing the Monimiaceae into two subfamilies, but recognized only four tribes.

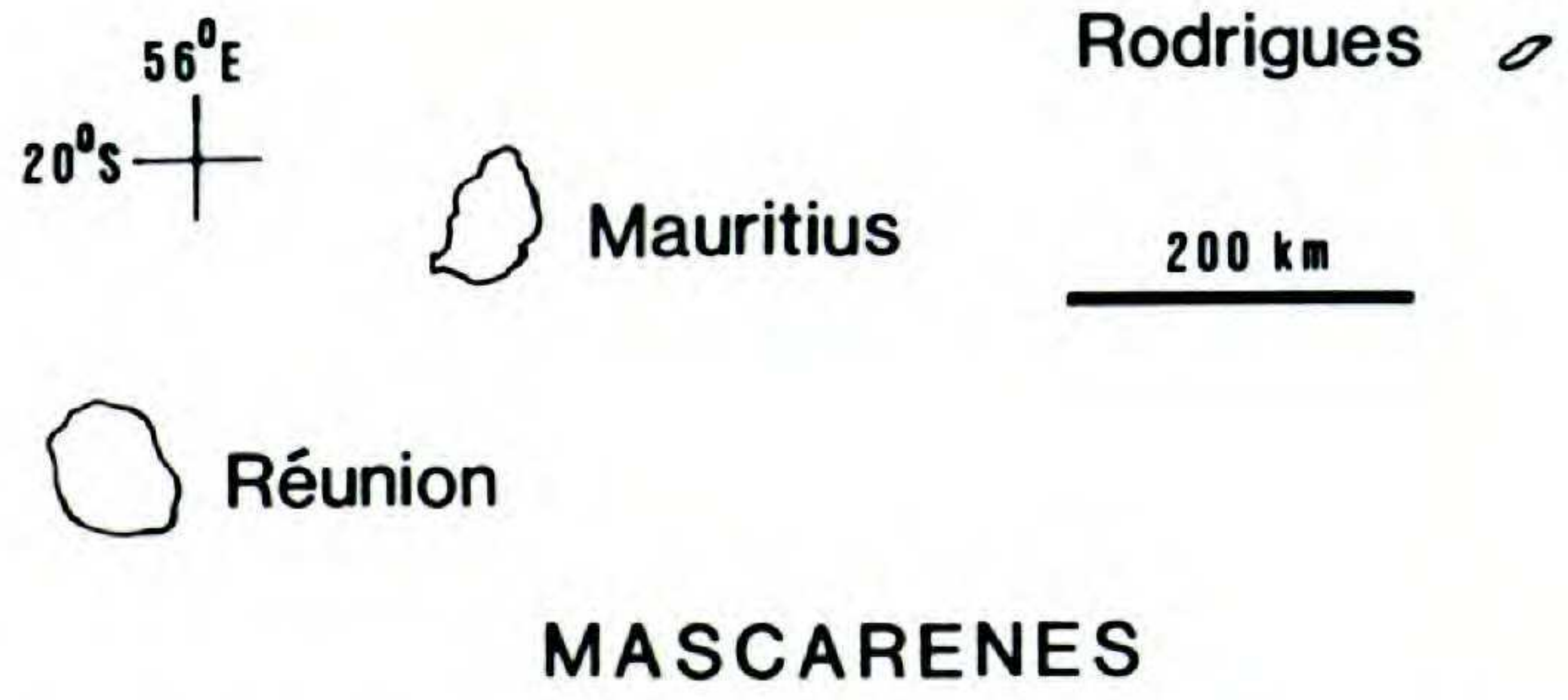


FIGURE 2. Regional map of study area, showing the Mascarene archipelago.

As a result of its extreme diversity, many attempts have been made to dissolve the Monimiaceae sensu lato (Brown, 1814; Lindley, 1853; Pichon, 1948; Schodde, 1970; Smith, 1969). The truly extraneous elements, however, notably *Amborella, Austrobaileya,* and Trimeniaceae, have been removed from the family by workers such as Pichon (1948) and particularly Money et al. (1950) in their important study of the morphology and relationships of the family. I agree with Thorne (1974) that the Monimiaceae sensu lato comprise a rather large and variable but coherent group with at least five major evolutionary lines derived from now extinct common ancestors. Recent morphological and anatomical studies by Sampson (1969a, 1969b), Endress (1980a, 1980b), as well as those by Money et al. (1950), support the rationality of treating these lines as subfamilies belonging to a single, diverse family rather than pursuing the alternative of splitting them into five separate families.

Hortonioideae, the smallest subfamily, contains three species in the unique genus *Hortonia* endemic to Sri Lanka (Ceylon). Its members possess an elaborate perianth with spirally arranged petaloid and sepaloid series, floral bisexuality, free stalked carpels borne on a discoid receptacle, basal staminal appendages, helical banded pollen, primitive wood anatomy, and the gametic chromosome number $n = 19$ (Money et al., 1950; Goldblatt, 1974; Endress, 1980a). Because it has retained the greatest assemblage of primitive characters, it has been considered to be most representative of the ancestral condition (Money et al., 1950), although recent studies by Endress (1980a) suggest it occupies a position intermediate between the Atherospermoideae and the Monimiaceae sensu stricto (i.e., Mollinedioideae plus Monimioideae of Thorne).

Members of the next subfamily, Atherospermoideae, are linked to the Hortonioideae by the similarly petaloid perianth and floral bisexuality of some members, and by their separate carpels borne on a shallowly concave receptacle. Advancements over the Hortonioideae include whorled arrangement of the parts and reduction in their number, and a tendency towards floral unisexuality. The Atherospermoideae are characterized by having bisporangiate valvate stamens, erect, basal ovules (usually), a single nodal trace, advanced wood anatomy, and a basic chromosome number of $x = 22$. These plants also possess 1–2-colpate pollen and show a trend towards specialized comose, wind-dispersed carpels. The five genera and 12 species of Atherospermoideae have a strongly disjunct austral distribution ranging from Australasia to Chile, emphasizing the subfamily's great antiquity.

The Siparunoideae are also characterized by bisporangiate valvate stamens, erect basal ovules, a single nodal trace and a basic chromosome number of $x = 22$. These features are similar to those found in the Atherospermoideae, and the two groups probably represent lines of parallel evolution from a common ancestral stock (e.g., Schodde, 1970). The Siparunoideae, however, lack the basal staminal appendages, septate wood fibers, and hippocrepiform sclerids of the Atherospermoideae. Furthermore, advanced trends such as vessels with simple perforation plates, and closed, reduced floral receptacles with a velum replacing the perianth occur in the Siparunoideae in addition to other differences such as inaperturate, granulate pollen and bird-dispersed carpels. The subfamily comprises three genera: *Siparuna* with about 160 species in tropical America, *Glossocalyx* with three species in west tropical Africa, and *Bracteanthus* with a single species in Brazil. Thorne (1974) suggested that *Bracteanthus* may merit tribal or subfamilial status, and that Glossocalyxoideae be recognized as a subfamily (Thorne, 1983).

The largest subfamily, Mollinedioideae, contains about 18 genera and over 145 species (Thorne, 1983). Its members are characterized by having apetalous, unisexual flowers displaying various degrees of reduction and specialization, relatively primitive wood anatomy, and gametic chromosome numbers of $n = 18, 19, 22$, ca. 38, ca. 43, and 57 for various genera (Goldblatt, 1974).

Thorne (1974) united *Monimia* (3 species, Mascarene Islands) with *Peumus* (monotypic, Chile) as the sole members of the subfamily Monimioideae. Both genera have paired basal appendages on the stamens; large, spinose pollen, and comparatively advanced wood anatomy. This seems to be the most rational placement of these two genera in light of the available evidence.

Although recent subfamilial revisions of the Monimiaceae have been adequate (e.g., Thorne, 1974), all have neglected treatment at the tribal level. As Perkins' (1911, 1925), Perkins and Gilg's (1901), and Hutchinson's (1964) treatments of the subfamilies and tribes are outdated, a critical reassessment of the subfamilies of Monimiaceae at the tribal level is urgently needed.

GEOLOGICAL HISTORY AND REGIONAL SETTING

Beginning with a Jurassic Gondwana supercontinent, the formation of the Indian Ocean commenced as Africa (with India and Madagascar) rotated away from South America at the start of the Cretaceous (summarized by Fisher et al., 1967). At the same time the Antarctica-Australia mass began drifting southward, whereas the block comprising Africa-India-Madagascar remained intact until the mid-Cretaceous prior to about 90 Ma (Raven, 1979). At that time Madagascar occupied a position against the present Kenya-Somalia coast and was part of a Malagasy-Mascarene subcontinent joined to India via the now largely submerged Mascarene Plateau (Axelrod & Raven, 1978). Separation of this subcontinent from Africa occurred during the mid- to late Cretaceous at about 90 Ma (Raven, 1979). Probable separation of India from the Malagasy-Mascarene subcontinent occurred at the onset of its northward movement, about 70 Ma, which continued until it collided with the Asian landmass at about 45 Ma (Raven, 1979).

Formation of the present crescent-shaped Mascarene Plateau began with the separation of a portion of continental crust from Madagascar in the late Cretaceous or early Tertiary as Madagascar moved southward (Fisher et al., 1967; Kutina, 1975; Wild, 1975). This fragment, composed of Precambrian granites, included the present Seychelles archipelago and possibly the entire western flank of the Mascarene Plateau above the Saya de Malha bank (Fisher et al., 1967). Formation of the remaining portion of the Mascarene Plateau from the Saya de Malha southward to Mauritius was probably accomplished by late Cretaceous-early Tertiary submarine volcanic extrusions (Fisher et al., 1967).

The Rodrigues Ridge, from which Rodrigues Island emerges, is parallel to a fracture zone extending eastward across the Midoceanic ridge complex and was probably formed during the late Tertiary (Fisher et al., 1967). It is a volcanic entity distinct from the Mascarene Plateau, separating the latter from Mauritius and Réunion (Fig. 2).

The Comore archipelago, situated between Madagascar and Africa (Fig. 1), is a product of successive Pliocene-Pleistocene volcanic eruptions (Esson et al., 1970). In contrast to Madagascar, which is a continental island, the Mascarenes and Comores are volcanic in origin and therefore strictly oceanic in nature.

GEOMORPHOLOGY AND CLIMATE

At present Madagascar is separated from the African mainland by the Mozambique channel, some 500 km wide at its narrowest point (Fig. 1). Situated midway between Africa and the northern part of Madagascar and separated on either side by depths of ca. 3,000 m are the four islands comprising the Comore archipelago: Mayotte, Anjouan, Mohéli, and Grande Comore. Stretching from ca. 800 to 1,600 km due east of Madagascar lies the Mascarene archipelago comprising the islands of Réunion, Mauritius, and Rodrigues. The Mascarenes are separated from the nearest landmass, Madagascar, by a stretch of ocean ca. 4,000–5,000 m deep.

MADAGASCAR

As the world's third largest island with an area of 590,000 km^2, Madagascar is truly continental in nature, consisting of a fragment of the original Gondwana landmass. Its large size, insular nature, and long isolation have made it an important refugium for many unique and relictual groups of plants and animals, including the lemurs. Its former connection to Africa and India once provided a route for Cretaceous dinosaurs and the rich angiosperm floras that appeared at that time (Raven & Axelrod, 1978).

Geologically, Madagascar is composed of four elements (Brenon, 1972). A much folded and outcropping metamorphic Precambrian basement in the form of a peneplain comprises the rugged central plateau which rises above 1,000 m (range 800–1,500 m) and also the highest mountains which are under 3,000 m (2,876 m at the Tsaratanana massif). This basement drops off abruptly along the great eastern escarpment down to a narrow coastal plain. Secondly, a slightly tilted Permo-Carboniferous continental sedimentary formation belonging to the Karroo system overlies the Precambrian basement and forms a band along the western third of the island. Thirdly, basaltic volcanic formations belonging to upper Cretaceous eruptions form extensive flows in parts of the eastern and western regions and have given rise to certain mountain complexes in the north, center, and south of Madagascar. Finally, weathering and laterization of the Precambrian basement has resulted in a mantle of lateritic clays averaging 10–15 m thick overlying the bedrock. This is undergoing massive erosion accelerated by historic removal of much of the island's vegetation by man.

Madagascar's diverse geomorphology is the result of submersion and uplifting, pedogenesis and erosion, and scattered vulcanism during its long history. This edaphic diversity coupled with a variety of climatic types has resulted in the wide spectrum of habitats that exists in Madagascar.

Madagascar's position, considerable size (590,000 km^2), and close juxtaposition of physical features such as lowland coastal plains gradually or steeply sloping to areas of medium altitude, and mountains exceeding 2,500 m elevation, are all responsible for its considerable climatic diversity (Donque, 1972).

First, its insular nature provides a maritime environment which is most prevalent in the eastern region. Here, warm oceanic currents moderate the temperature while moisture-laden trade winds and tropical cyclones impinging upon the east coast deposit heavy rains along the coast and eastern escarpment, permitting the development of dense, evergreen wet forest which forms a zone along the eastern third of Madagascar.

Second, Madagascar is sufficiently long (ca. 1,500 km) and wide (ca. 450 km average) to display many characteristics of a small continent. This continentality is reflected in a wide spectrum of temperature, atmospheric humidity, precipitation, and wind regimes. As a result of its longitudinal extension, the island possesses subequatorial regions in the north (at 12°S) where a monsoon climate and dry season modify the composition of the evergreen forest. In the south, it passes through the Tropic of Capricorn and extends into the subtropics at its southern extremity (25°30′S), giving rise to considerable thermal variation. On a latitudinal basis, both precipitation and temperature decrease considerably in the central uplands. Precipitation further decreases and temperature increases to the west and south as the Trade winds rapidly lose their remaining moisture and velocity due to the rain shadow effect. As a result, the vegetation

TABLE 1. Distribution of total Monimiaceae and *Tambourissa* species per island in the Malagasy region in relation to area, elevation, and age of island.

Island	Area (km²)	Elevation (m)	Age (Ma)	Total Species Monimiaceae	Total Species *Tambourissa*
Madagascar	590,000	3,000	70† (as island)	35	26
Réunion	2,500	3,000	3.0	5	2
Mauritius	1,865	900	7.8	11	10
Grande Comore	1,148	2,400	0.01†	1	1
Anjouan	424	1,600	1.5	2	2
Mayotte	370	700	3.7	1	1
Mohéli	290	800	ca. 1.5	1	1
Rodrigues	110	400	1.5	0	0

becomes progressively more xeric in nature to the south and west, passing from sclerophyllous evergreen forest to semideciduous forest and finally thorn scrub and desert (Koechelin et al., 1974, give a detailed account of the vegetation).

Temperature, wind, and rainfall are further influenced by the island's varied relief, giving rise to a spectrum of bioclimates varying in both temperature and precipitation. For example, some of the higher mountains extend into the cloud zone and harbor a montane cloud forest formation, above which occurs a low, ericoid scrub characteristic of the high montane zone.

This diversity of habitats and extreme ecological gradients in conjunction with Madagascar's long isolation have resulted in high levels of floristic endemism: up to 48% of the genera and 95% of the species are endemic in certain regions (Koechelin et al., 1974; Leroy, 1978). It is therefore not surprising that Madagascar harbors the greatest constellation of Monimiaceous taxa in the region (three genera and ca. 35 species), Africa notwithstanding (Table 1).

MASCARENE ARCHIPELAGO

The three Mascarenes are volcanic oceanic islands that consist of the exposed summits of submarine mountain chains, i.e., Mauritius and Rodrigues, and an isolated volcano arising from an abyssal submarine plain, i.e., Réunion (Cadet, 1977).

All three islands experience a tropical insular climate moderated by the maritime effects of the warm ocean and the steady south-east Trade wind regime. Precipitation is most abundant during the warm and rainy austral summer season lasting from December to April, occurring as orographic rains resulting from adiabatic air expansion, and also as heavy cyclonic rains. In addition to bringing rain, cyclones, with winds gusting up to 240–320 km/hr, are often destructive to the vegetation. On the average, direct hits by cyclones occur only once every 12 to 15 years. The relatively drier and cooler austral winter season lasts from May to November.

The mean annual precipitation ranges from 1,100 to 1,700 mm in Rodrigues (Lorence, 1976), and from 1,000 to 5,000 mm in Mauritius and Réunion (Lorence, 1978; Cadet, 1977). Mean annual temperatures in the Mascarenes are not extreme, ranging from 16 to 20°C in the uplands and from 21 to 25°C in the lowlands during the winter, and from 21 to 25°C in the uplands and 27 to 30°C in the lowlands during the summer.

Réunion, the largest (2,500 km²) and easternmost of the Mascarene Islands, is the summit of a volcanic cone rising some 3,000 m above sea level. Its active volcano, Piton de la Fournaise, still erupts frequently, emitting basaltic lavas similar to the Pleistocene flows in Mauritius (Fisher et al., 1967). Quaternary lavas from the Piton des Neiges flows have been dated at 2.1 Ma, although Fisher et al. (1967) suggest that submerged caldera flows may be older, possibly ca. 3 Ma (Cadet, 1977). Some subsidence appears to have taken place during the Quaternary, perhaps resulting in a small reduction of the island's surface area. Coral reef development around Réunion is virtually absent.

In addition to its accentuated relief, Réunion's 3,000 m altitude provides the greatest range of habitats of any of the Mascarenes, ranging from semideciduous dry forest and thicket in the western rain shadow, to lowland wet forest, montane cloud forest and high montane ericoid scrub and grassland. *Tambourissa,* with only two species here, is less abundant and much less diverse than in Mauritius (10 species; Table 1). It is significant, however, that *Monimia* reaches its greatest diversity and abundance here, with three species often forming locally abundant or dominant elements of the wet and cloud forest formations. Much of the upland vegetation in Réunion is still intact, but little remains in the lowlands.

Mauritius, the central island, is second largest with an area of 1,865 km^2 and a maximum altitude just under 900 m. By far the oldest of the three Mascarenes, its earliest lavas are Pliocene, dating to 7.8 Ma (McDougall & Chamalaun, 1969), and its vulcanism ended about 100,000 years ago during the Pleistocene. During its long history, erosion has moderated the island's relief which consists of a central plateau fringed by a discontinuous mountain range dipping down to coastal plains in all but the southern sector. Except for its well-developed fringing coral reefs, Mauritius is completely volcanic in origin and composed of alkali olivine basalts deposited in three main strata. The presence of coral deposits at altitudes of up to 100 m above sea level on the mainland suggests past fluctuations in the sea level, although progressive subsidence seems to be the case (Fisher et al., 1967). If the submarine plateau surrounding Mauritius is taken into consideration, the island's previous area was probably ca. 2,500 km^2 during the lowered sea levels of the Quaternary (comparable to Réunion's present area), as opposed to its 1,865 km^2 today. It seems that earlier in the island's history its relief was more accentuated than today but probably did not exceed 1,000 m in altitude during the last 3.5 Ma (Cadet, 1977).

Mauritius supports a fairly diverse array of plant communities, notably semideciduous dry forest in the western rain shadow area, lowland and lower montane evergreen wet forest, small areas of cloud forest on the highest mountains, and patches of heath formation (Lorence, 1978).

Next to Madagascar, Mauritius harbors the most species of *Tambourissa* (10). In contrast, *Monimia,* which is essentially a genus of cloud forests, is poorly represented with a single species in Mauritius, perhaps because of its low altitude. Representative areas of most of the island's plant communities are still preserved by way of nature reserves and crown land, but many of these have been irreversibly degraded by invasive exotic plant species.

Rodrigues is the smallest and westernmost of the Mascarenes, with an area of only 110 km^2 and an altitude just under 400 m. A ridge composed of a uniform series of alkali olivine basalt flows whose exposed parts do not exceed 1.54 Ma (McDougall et al., 1965), it has apparently undergone extensive subsidence since its formation and probably once occupied nearly ten times its present area (Cadet, 1977). Now only the summit of a large submarine platform remains exposed, supporting large, well-developed fringing coral reefs. In view of its high specific level of floristic endemism, equalling the other two Mascarenes, Rodrigues could be older than Réunion but younger than Mauritius (Cadet, 1977), contrary to the suggestion put forth by McDougall et al. (1965).

Because of its small size and low elevation, Rodrigues is ecologically the least diverse of the Mascarenes. Most of the island was once covered by a low evergreen moist or wet forest, drier on its leeward western side, although sections of uplifted coralline calcarenite support an interesting scrub formation. Although a species of *Monimia* was supposedly collected in Rodrigues, no substantiated records of Monimiaceae are known from the island. This is probably because of its isolation and paucity of the proper habitats. Also, nearly all of Rodrigues' indigenous vegetation has been destroyed by man.

COMORE ARCHIPELAGO

The Comores are a group of four volcanic islands located in the Mozambique channel midway between Madagascar and Mozambique on the east African coast. Situated on a submarine ridge, they are the product of successive volcanic eruptions extending from southeast to northwest and are no older than the Pliocene-Pleistocene (Guilcher et al., 1965; Hajash & Armstrong, 1972). Analogous to the Mascarenes, the Comores differ in being more closely spaced (separated by distances no greater than 65 km; Fig. 1), are closer to major landmasses, and are on the average smaller and younger (Esson et al., 1970).

Mayotte is the most southeasterly, the oldest (ca. 3.65 Ma), and most highly eroded of the four islands. With an area of 370 km^2 and a maximum altitude of 660 m, it consists of a succession of old lava flows from at least two volcanic eruptions (basaltic and phonolitic) which gave rise to the bulk of the island. Following periods of relative stability, a final period of vulcanism poured lava across the eastern part of the island. Other indications of Mayotte's relatively advanced age within the archipelago are a highly embayed coastline, development of the finest barrier reef and lagoon in the Indian Ocean, and occurrence of deep, red laterized soils (Guilcher et al., 1965).

Anjouan and Mohéli are both centrally located and represent the summits of extinct volcanos. Both are relatively old structures with eroded but still recognizable craters and cones. Anjouan is larger, attaining 1,595 m, and has an area of 424 km² with an accentuated relief and narrow but fringing coral reefs emcompassing about two-thirds of the coastline. Its oldest lavas have been dated at 1.52 Ma (Hajash & Armstrong,1972). Mohéli is the smallest of the Comores, rising to 790 m altitude with an area of only 290 km². Its relief is less rugged but its reefs are also wide and well developed, although its lavas have not been dated. Mayotte, Anjouan, and Mohéli are all volcanically extinct.

Grande Comore, largest (1,148 km²) and youngest of the four islands, has an active volcano whose summit attains 2,360 m, and is essentially a mass of scarcely eroded lava lacking permanent rivers and streams. The only dated lavas from Grande Comore are recent (0.01 Ma), although underlying flows are thought to be older (Hajash & Armstrong, 1972). Coral reef development around the island is sparse and embryonic, also reflecting its relative youth.

The Comores lie in the south-east Trade wind belt, although they are somewhat sheltered by Madagascar, and cyclones are rare. The drier and cooler winter season extends from May to October, the majority of the rain falling during the hot austral summer season from November to April (Manicacci, 1939). In 1935, the following annual rainfalls were recorded: Grande Comore, 4,254 mm; Anjouan, 1,411 mm; Mayotte, 869 mm (at Dzaoudzi, but probably double inland); Mohéli, 478 mm (Manicacci, 1939). Temperatures range from 25 to 35°C in the summer and from 18 to 25°C in the winter, depending on the elevation.

The Comores generally support evergreen moist or wet forest on their lower windward and mountainous slopes, and semideciduous dry forest in the low altitude regions of the rain shadow. Anjouan and Grande Comore have zones of cloud forest above 900 or 1,000 m, and this gives way to *Philippia* heath formation on the Karthala volcano massif on Grande Comore. Each island has but a single species of *Tambourissa,* except for Anjouan which has two (Table 1). Four of the five Comorean species of *Tambourissa* appear to be closely related and may be derived from a common ancestor.

BIOGEOGRAPHY AND DISTRIBUTION

Biogeographically, it appears that direct migration of the Monimiaceae between Africa and South America occurred by the Eocene, after which widespread extinction took place in Africa (Raven & Axelrod, 1974; Axelrod & Raven, 1978). Fossils that have been considered Monimiaceous are known from the late Cretaceous (ca. 70–80 Ma) in Europe, Africa, and Argentina. In contrast to the widespread floral and faunal impoverishment that took place in continental tropical Africa (Richards, 1973, 1979), the Malagasy region provided an important refuge for many elements of the area's biota; for example, the lemurs in Madagascar and the Comores, and the now extinct flightless birds such as the dodo and solitaire in the Mascarenes (Carlquist, 1965).

The Monimiaceae may be thought of as botanical counterparts of the lemurs and are represented by four genera and about 55 species in the Malagasy region, all endemic. The isolation and habitat diversity offered by islands are well known to be conducive to rapid adaptive radiation (e.g., Carlquist, 1965, 1974), which is exemplified by the Malagasy area Monimiaceae. In marked contrast, only two genera of Monimiaceae have persisted in continental Africa—i.e., *Glossocalyx* and *Xymalos*—comprising a total of four species. This is primarily because the Monimiaceae attain their greatest diversity in premontane wet and montane cloud forest formations, habitats that are abundant in the Malagasy region but poorly represented in Africa. Furthermore, most cannot tolerate the ecologically significant dry periods that are characteristic of even the wet forest in Africa (Richards, 1973), although their absence from the cloud forests of the east African mountains is puzzling. Perhaps these forests were greatly reduced in extent during the dry periods of the Pleistocene, and Monimiaceae were unable to recolonize them from their more equable refuge areas on Madagascar and the Mascarenes.

Madagascar harbors three closely allied genera of trees and shrubs belonging to the subfamily Mollinedioideae. Of these, *Ephippiandra* (6 spp.) and *Decarydendron* (3 spp.), are endemic. Their inability to spread to the other islands may be a reflection of their poor dispersibility or seed viability. Alternatively, suitable habitats may be lacking on the satellite islands. This does not appear to be the case, however, because relatively large and elevated islands such as Réunion and Mauritius offer many of the same habitats as Madagascar (Table 1).

Tambourissa, however, has reached six of the seven satellite islands where it has become established and undergone successful adaptive radiation (Table 1). Reports that *Tambourissa* occurs in Java (e.g., Cavaco, 1965) appear to be erroneous (see discussion under *T. ficus*), and the genus appears to be restricted to the Malagasy floristic region. Possible reasons for its success most likely include its bright red-orange drupes, which are ostensibly more attractive to birds (those of *Ephippiandra* ripen black) resulting in greater dispersibility, a greater seed viability (drupes of *Tambourissa* may take two or three months to germinate; D. Lorence, pers. observ.), and enhanced ability to compete and evolve rapidly. In any case, *Tambourissa* provides an excellent model for island evolution in a family of primitive angiosperms.

Monimia (Monimioideae) consists of three closely related species endemic to the Mascarene Islands of Mauritius and Réunion. Its absence from Madagascar is puzzling in view of its bird-dispersed carpels. *Peumus* in Chile appears to be its closest relative, although it also shares a number of features with *Palmeria* from Oceania (see discussion under *Monimia*).

HABITAT AND ECOLOGY

The majority of ecological and floristic studies or surveys conducted for the islands of the Malagasy region demonstrate or at least mention the importance of the Monimiaceae as woody elements of the vegetation (Vaughan & Wiehe, 1937, 1941; Humbert, 1965; Legris, 1969; Koechlin, 1972; Koechlin et al., 1974; Cadet, 1977). In addition, data from specimens provide much information.

MADAGASCAR

Although I am unaware of any specific ecological studies for Madagascar involving Monimiaceae, the broad vegetational surveys of Humbert (1965) and Koechlin et al. (1974) coupled with data from specimens which I have examined and those cited by Cavaco (1959) have enabled the habitat and distribution of most species to be established. A significant number of taxa, however, are known from only one or several collections, possibly a result of undercollecting, which may therefore inaccurately portray their actual distributions. Of the Imperfectly Known *Tambourissa* species, only numbers 40 (*T.* sp. A) and 42 (*T.* sp. C), are included in this discussion, because collection localities for the others are either too vague or were not located.

Work done by Humbert (1965) and Koechlin et al. (1974) indicates that in Madagascar species of *Tambourissa,* along with *Weinmannia* (Cunoniaceae), are among the most frequent and characteristic components of the canopy in the montane wet/cloud forest zone. *Tambourissa* attains its greatest diversity here, with at least 14 of the island's 26 species occurring in this zone (Table 2) which forms a belt along the eastern part of the island from ca. 800 m and extends upward to the mountains of the central plateau to between 1,300 and 1,800 m. Annual precipitation here ranges from ca. 1,000 to 2,000 mm, with a short dry season.

In addition to *Tambourissa,* two endemic Madagascan genera also occur in this zone, *Decarydendron* (2 spp.) and *Ephippiandra* (3 spp.), bringing the total number of Monimiaceae to 19 (Table 2). The *Tambourissa/Weinmannia* zone is clearly Madagascar's richest habitat in terms of Monimiaceae species and genera.

In the east, this zone is subtended by a lowland wet forest of Myristicaceae and *Anthostema* (Euphorbiaceae) receiving an annual precipitation of ca. 1,500–3,500 mm and having no significant dry season. In addition to sharing about three species with the former zone, including *Ephippiandra madagascariensis* and two species of *Tambourissa,* this zone possesses a number of its own species, most notably *Decarydendron lamii* and five species of *Tambourissa*: *T. alaticarpa, T. castri-delphinii, T. decaryana, T. longicarpa,* and *T.* sp. C. Besides *T. castri-delphinii,* the wide-ranging *T. purpurea* and *T. religiosa* are the only Monimiaceae known to inhabit the coastal forests on sand dunes.

The lowland wet forest also extends to the small Sambirano region in the northwest, including Nosy Be Island, where it is further characterized by the presence of many Chlaenaceae, an endemic family. In addition to harboring such wide-ranging species as *Ephippiandra madagascariensis* and *Tambourissa purpurea,* the Sambirano area has two endemics: *T. nitida* and *T. nosybensis.*

At altitudes from ca. 1,800 to 2,000 m in the cloud zone on the mountains of the central re-

TABLE 2. Distribution of Monimiaceae according to habitat in Madagascar.

1. Lowland wet forest zone of Myristicaceae and *Anthostema* (ca. 0–800 m), including littoral forest and Sambirano region.
   - *Decarydendron lamii*
   - *Ephippiandra madagascariensis*
   - *Tambourissa alaticarpa*
   - *T. castri-delphinii*
   - *T. decaryana*
   - *T. longicarpa*
   - *T. nitida*
   - *T. nosybensis*
   - *T. perrieri*
   - *T. purpurea*
   - *T. religiosa*
   - *T.* sp. C (no. 42)
2. Medium altitude wet/cloud forest zone of *Tambourissa* and *Weinmannia* [ca. 800–1,300(–1,800) m].
   - *Decarydendron helenae*
   - *D. perrieri*
   - *Ephippiandra domatiata*
   - *E. madagascariensis*
   - *E. microphylla*
   - *Tambourissa beanjadensis*
   - *T. capuronii*
   - *T. floricostata*
   - *T. gracilis*
   - *T. hildebrandtii*
   - *T. humbertii*
   - *T. madagascariensis*
   - *T. perrieri*
   - *T. purpurea*
   - *T. religiosa*
   - *T. thouvenotii*
   - *T. trichophylla*
   - *T. uapacifolia*
   - *T.* sp. A (no. 40)
3. Sclerophyllous montane lichen forest zone (central mountains, 1,300–2,000 m).
   - *Ephippiandra myrtoidea*
   - *E. perrieri*
   - *E. tsaratanensis*
   - *Tambourissa gracilis*
   - *T. parvifolia*
4. High montane *Philippia* ericoid heath formation (central mountains, above ca. 2,000 m).
   - *Ephippiandra microphylla*
   - *E. perrieri*
   - *Tambourissa parvifolia*
5. Sclerophyllous moist forest zone of *Uapaca bojeri* and Chlaenaceae (western slopes of central domain, up to ca. 800–900 m).
   - *Tambourissa hildebrandtii*
   - *T. purpurea*

TABLE 2. Continued.

6. Semideciduous dry forest zone of western domain (below ca. 700–800 m).
   - *Tambourissa bathiei* (probably riverine)
   - *T. perrieri* (probably riverine)

gion, the *Tambourissa/Weinmannia* belt is replaced by a dense sclerophyllous forest with an abundance of epiphytic lichens. Perhaps because of the lower temperatures, the Monimiaceae drop out rapidly here (Table 2). *Ephippiandra microphylla* and *Tambourissa gracilis* are virtually the only species shared with the zone below. The only species characteristic of this zone and, to a lesser extent, of the high montane ericoid thicket superseding it beyond the cloud zone at above ca. 2,000 m are *Ephippiandra myrtoidea, E. perrieri, E. tsaratanensis,* and *Tambourissa parvifolia.*

The western slopes of the central plateau at and below ca. 800–900 m are characterized by a hotter, drier climate with more extreme temperatures. This area supports sclerophyllous forest of *Uapaca bojeri* (Euphorbiaceae) and Chlaenaceae, with only *Tambourissa hildebrandtii* and *T. purpurea,* two of the most widespread species, able to persist here.

In the dry western regions that extend to the coast, the sclerophyllous forest is gradually replaced by a semideciduous dry forest of *Dalbergia, Commiphora,* and *Hildegardia.* The only Monimiaceae found here are *Tambourissa bathiei* and *T. perrieri,* which apparently occur in riverine forests.

It should be emphasized that the vegetation of Madagascar, like most of the other islands, has undergone and continues to undergo severe degradation and destruction under the influence of man (Rauh, 1979). Because of its size, however, remnants of most and even fairly extensive areas of some vegetation types still remain (Rakotozafy, pers. comm.), but the need for their conservation is essential.

MASCARENE ISLANDS

On the average larger and older than the Comores, the Mascarene Islands also harbor more genera (two) and species (15) of Monimiaceae despite their greater isolation. In addition, the Mascarenes have been comparatively well studied floristically (Baker, 1877; Balfour, 1879; Cordemoy, 1895; "Flore des Mascareignes," in progress) and ecologically (Vaughan & Wiehe, 1937, 1939, 1941; Wiehe, 1949; Rivals, 1952; Cadet, 1977), thus permitting a more definitive assessment of the family's status there.

RÉUNION

Réunion is analogous to Grande Comore in being the only volcanically active member of its archipelago but is larger and older, supporting two genera and five species of Monimiaceae in contrast to the latter's unique species. Cadet's (1977) comprehensive study of the island's vegetation emphasizes the importance of the family as woody components of the flora. Although harboring the greatest expanse of indigenous forest of the three Mascarenes, many areas of Réunion are undergoing a dramatic invasion by vigorous exotic species such as *Psidium, Rubus,* and *Furcraea,* similar to that occurring in the other two islands.

Much of Réunion's lowland forest has disappeared, particularly in the dry western sector. Fairly extensive areas of lowland wet forest ("forêt mégatherme hygrophile" sensu Cadet, 1977) still remain above ca. 300 m, however, on the southern slopes of the active volcano, Piton de la Fournaise (at Mare Longue, Brûlé de Baril and other areas). Here a lush wet forest dominated by Sapotaceae (*Labourdonnaisia, Mimusops,* and *Sideroxylon*) has become established on the mosaic of lava flows where the rainfall averages 4,000–5,000 mm per year. *Tambourissa elliptica* subsp. *micrantha* appears here at ca. 300 m as a local, occasional to common component of the middle and upper strata and ranges to the mid or rarely upper limits of the wet forest zone (ca. 800–1,000 m) where it is generally replaced by *T. elliptica* subsp. *elliptica.* The latter is characteristically a smaller understory tree or treelet of occasional to common occurrence in both the wet forest zone below 1,100 m and the cloud forest zones (ca. 1,100–2,000 m) (Fig. 31).

The only other species to occur in the lowland wet forest zone of Réunion is *Monimia ovalifolia,* which appears at ca. 500 m and extends to ca. 1,700 m in the cloud forest zone. It typically forms local populations on sheltered slopes and in valleys and may become a canopy tree.

The lower limits of the cloud belt lie at ca. 800–1,100 m and mark the transition from wet to cloud forest ("forêt mésotherme hygrophile" of Cadet), a zone characterized by lower temperatures and relatively constant high humidity. It is in the cloud forests of Réunion that *Monimia* attains its greatest abundance and diversity. The climax is considered to be the *Monimia/Dombeya* association ("Bois de couleurs") although *Acacia heterophylla* Willd. is dominant in some areas (Cadet, 1977).

Of the three *Monimia* species occurring in this zone, *M. rotundifolia* is by far the most abundant and widespread, codominant in many areas with species of *Dombeya* (Sterculiaceae) and other genera, e.g., at Col de Bellevue and Bébour forest (Fig. 22). Mature individuals 8–16 m high with dense, spreading crowns are often major components of the mid stratum and canopy. It occurs less frequently in the *Acacia/Nastus* forest and occasionally in *Philippia* heath up to ca. 2,000 m, with its lower limit extending down to ca. 1,000–1,100 m at the interface with lower altitude wet forest.

Monimia amplexicaulis is more restricted in distribution than *M. rotundifolia* and is generally confined to the mid and upper limits of the cloud forest, occasionally with *Acacia.* It characteristically forms discrete populations on the sheltered, leeward escarpments of the "cirques" or ancient volcanic calderas and is known primarily from the following localities where it usually replaces *M. rotundifolia*: Hauts du Tévelave, Plaine des Cafres, and Cirque de Cilaos (Fig. 22). An example of ecological differentiation between the two species was studied at Hauts du Tévelave, where *Monimia amplexicaulis* begins to replace *M. rotundifolia,* which occurs alone below ca. 1,700 m. Here, both species occur sympatrically at ca. 1,700 m along the Domanial line (Ligne Dominicale); neither intermediates nor hybrids were observed among dozens of individuals examined. The two species are easily recognized in the field and appear to maintain their integrity by flowering at different times.

Monimia ovalifolia is an occasional tree up to ca. 1,700 m altitude but is rarely abundant. It occurs sympatrically with *M. rotundifolia* in many localities, e.g., at Bébour forest where both species remain distinct and have different flowering times (Fig. 22).

Only two species of *Tambourissa* occur in the cloud zone: *T. crassa* and the macrophyllous upland form of *T. elliptica* subsp. *elliptica. Tambourissa crassa* is a light-demanding small tree which occupies the upper stratum of low forest or occurs in relatively open mixed heath at 1,200–

TABLE 3. Occurrence of Monimiaceae species according to habitat in Mauritius: indigenous plant communities.

	Philippia Heath:	*Sideroxylon* Wet Forest:		High Forest:		Cloud Forest:	Semideciduous Dry Forest:
	Pétrin; 660 m, pptn. 4,000 mm	Pieter Both; 550 m, pptn. 2,400 mm	Bel Ombre; 300 m, pptn. 2,400 mm	Macabé; 660 m, pptn. 3,200 mm	Brise Fer; 600 m, pptn. 2,400 mm	Mt. Cocotte; 760 m, pptn. 5,000 mm	Yemen; 200 m, pptn. 1,600 mm
Monimia ovalifolia						X	
Tambourissa amplifolia			X	X			
T. cocottensis						X	
T. cordifolia	X						
T. ficus		X		X	X	X	
T. pedicellata		X		X			
T. peltata	X	X	X	X	X	X	
T. quadrifida							X
T. sieberi				X		X	
T. tau	X		X	X		X	
T. tetragona						X	

2,000 m. *Tambourissa elliptica* subsp. *elliptica* is a slender, sciaphilous understory forest treelet (1,100–2,000 m). Both species are occasional woody elements of the cloud forest (Fig. 31).

On the tops of exposed crests and at altitudes above ca. 1,700–2,000 m the cloud forest gives way to a low ericoid heath formation dominated by *Philippia*, as in Madagascar and Grande Comore. Apart from the occasional occurrence of *Monimia amplexicaulis, M. rotundifolia, Tambourissa crassa,* and *T. elliptica* subsp. *elliptica,* whose upper ranges end here, no species are specially adapted to the heath formation. Likewise, no species are known to be adapted to the semideciduous dry forest ("forêt mégatherme" of Cadet) in the island's dry, leeward western sector (annual precipitation 800–1,500 mm).

In essence, Réunion's extensive cloud forests have favored adaptive radiation in the genus *Monimia,* which comprises three of its five Monimiaceae species. *Monimia rotundifolia* is the most widespread and abundant species, constituting a woody element of major importance in the cloud forest zone. *Tambourissa,* with two species, has not undergone the extent of adaptive radiation here that has occurred in Mauritius and Madagascar, although seemingly suitable habitats exist. This may be attributable to its more recent arrival, or to the island's younger age. That *Tambourissa* is undergoing adaptive radiation in Réunion is evident by the presence of two closely related species, one with two subspecies occupying different ecological zones.

MAURITIUS

Geologically the oldest of the Mascarene Islands, Mauritius has probably undergone considerable reduction by erosion since its inception, being slightly smaller and only a third as high as Réunion. Since the island's colonization by man almost 400 years ago, its original vegetation has been removed from nearly every accessible surface and has also undergone extreme degradation by introduced biota. Tracts representing most of the island's original vegetion still remain, however, in the form of nature reserves and crown land which comprise ca. 5–6% of its superficies (Lorence, 1978). Unfortunately, virtually all have been invaded by introduced plants such as *Furcraea, Ligustrum, Psidium, Rubus,* and many others, not to mention introduced animals (monkeys, stag, pigs) and birds (sparrows, mynahs, bulbuls), which help spread seeds of the exotic plants. All are contributing to the inevitable disappearance of the remaining native flora and fauna (Vaughan, 1968; Siegfried & Temple, 1975; Jolly, 1982; Pasquier & Jones, 1982).

The majority of forested areas remaining in the uplands (precipitation 2,000–5,000 mm) are occupied by floristically rich wet forest of variable composition but usually characterized by the presence of *Sideroxylon cinereum* Lam., *S. puberulum* A.DC., and other Sapotaceae such as *Labourdonnaisia* (the "*Sideroxylon* thicket" of Vaughan & Wiehe). Remnants of this formation extend down to ca. 200 m in some areas (e.g., at Bel Ombre) where up to three species of *Tambourissa* occur: *T. amplifolia, T. peltata,* and *T. tau* (Table 3; Figs. 38, 40).

In addition to the above, species such as *Tambourissa ficus* and *T. pedicellata* appear at higher altitudes, e.g., at Pieter Both Mt. (Table 3). Vaughan and Wiehe's (1941) detailed study of the *Sideroxylon* formation at Perrier Nature Reserve revealed that two individuals of *Tambourissa peltata* and 16 of *T. tau* occurred in a 1,000 m^2 plot (Table 4), and family dominance at Perrier was only 0.47%, lowest of the three sites (Table 4). My survey of populations of these two species in the same area shows 26 individuals of *T. peltata* per 12,700 m^2 (= 21/ha) and 57 individuals of *T. tau* per 512 m^2 (= 1,113/ha) (Fig. 3). The higher figure for the latter species, an understory treelet, suggests aggregation into much denser populations than *T. peltata,* a more highly dispersed canopy tree. Population density of these two species appears to correspond to their pollinator strategies (see discussion under Floral Biology).

On parts of the upland plateau and in some sheltered valleys the *Sideroxylon* formation passes into a high forest ("climax forest" of Vaughan & Wiehe). Vaughan and Wiehe's (1939, 1941) studies of the high forest at Macabé revealed the presence of 41 individuals 10 cm or more DBH belonging to three species of *Tambourissa* in a one hectare plot. In another 1,000 m^2 sample plot at Macabé, the genus was found to comprise 2.67% of the total number of individuals 10 cm or more DBH, with the following breakdown: *T. sieberi,* 13 (upper stratum tree); *T. ficus* (as *T. elliptica*), four (mid stratum tree); *T. pedicellata,* 28 (mid stratum tree; my survey in 1979 failed to show this species at Macabé); *T. tau* (as *T. amplifolia*), one (understory treelet). In addition, I found *T. amplifolia* to be a rare understory treelet or small tree at Macabé in 1979 (Table 3).

A comparable survey was carried out in somewhat drier high forest at Brise Fer (Table 3) several kilometers to the west of Macabé (Lorence et al., in prep.). Only two species of *Tambourissa* were found here, *T. ficus* and *T. peltata,* presumably due to the lower rainfall. Both showed up in our study at the rate of two individuals 25 mm or more DBH per 1,000 m^2.

TABLE 4. Comparative frequency of *Tambourissa* species in three uplant plant formations in Mauritius (adapted from Vaughan & Wiehe, 1941).

	Number Individuals per 1,000 m^2		
Species	*Philippia* Heath (Pétrin)	*Sideroxylon* Wet Forest (Perrier)	Macabé High Forest
T. cordifolia	44	—	—
T. ficus	—	—	4
T. pedicellata	—	—	28
T. peltata	1	2	—
T. sieberi	—	—	13
T. tau	—	16	1
Total	45	18	46
% Family dominance	2.04	0.47	2.67

Because of the island's low altitude, cloud forest only occurs on the flanks and summits of its highest mountains in areas of high rainfall (ca. 4,500–5,000 mm). In their study of the cloud forest (as "mossy forest") on Mt. Cocotte, Vaughan and Wiehe (1937) recorded only two species of *Tambourissa* in a 40 m^2 transect: *Tambourissa sieberi,* three individuals; *T. tau* (as *T. amplifolia*), two individuals. My survey of the summit of Mt. Cocotte in 1979 (unpubl. data) revealed the presence of five additional species: *Monimia ovalifolia, Tambourissa cocottensis* (endemic to the mountain), *T. ficus, T. peltata,* and *T. tetragona* (also endemic to the mountain) (Table 3). Mt. Cocotte harbors the highest concentration of Monimiaceae in the entire island, with seven of its 11 species found here. A survey of the cloud forest on Mt. Lagrave revealed a comparable situation, with six species present.

Another consequence of the island's low altitude is the paucity of *Philippia* heath formation in Mauritius, which occurs in small patches at only a few edaphically suitable areas such as Pétrin and Mt. Laselle. Formations of this type are restricted to areas of unweathered, highly ferruginous ground water laterite or "cuirasse," so called because of its impermeability to water. Although receiving a high rainfall (4,000 mm at Pétrin), the laterite is nearly devoid of true soil, and the heath formation is exposed to constant drying winds. As a result, most woody species possess xeromorphic leaves (microphyllous, sclerophyllous, or variously pubescent).

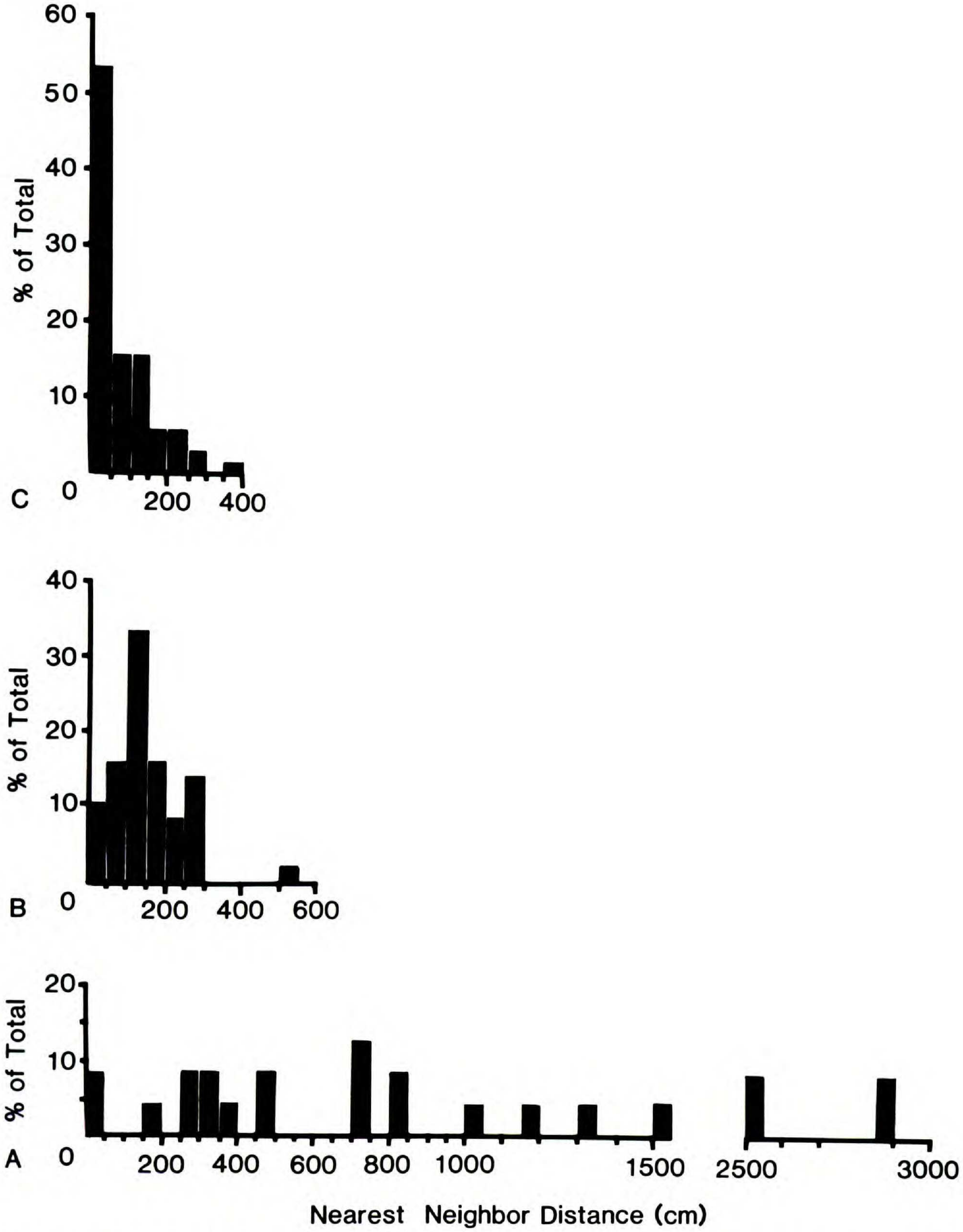


FIGURE 3. Nearest neighbor distance as percent of population for three species of *Tambourissa* studied in Mauritius, 1978–1979.—A. *T. peltata*, Perrier Nature Reserve, sample area = 12,700 m^2, N = 26 individuals, estimated frequency per hectare = 21.—B. *T. tau*, Perrier Nature Reserve, sample area = 512 m^2, N = 57 individuals, estimated frequency per hectare = 1,113.—C. *T. cordifolia*, Pétrin Nature Reserve, sample area = 410 m^2, N = 69 individuals, estimated frequency per hectare = 1,684.

Only a single species of Monimiaceae has successfully adapted to this environment: *Tambourissa cordifolia*, a low dioecious shrub with small, sessile coriaceous leaves. It is peculiar in being the only truly shrubby member of the genus known to me. In their study of a 1,000 m^2 transect at Pétrin, Vaughan and Wiehe (1941) found 44 individuals of *T. cordifolia*. My study of a population of the species at the same locality gave a much higher density (Fig. 3), 69 individuals per 410 m^2 (= 1,684/ha), suggesting the species is aggregated into dense, local populations. *Tambourissa cordifolia* also occurs in a few other regions with similar edaphic conditions, e.g., Mt. Laselle, Les Mares, and Mare Longue Plateau (Fig. 40).

Although *Tambourissa peltata,* and to a lesser degree *T. tau,* also occur in the heath formation at Pétrin, they are only marginally successful and occur as depauperate, stunted individuals. In their 1,000 m^2 sample, Vaughan and Wiehe (1941) only found a single individual of *Tambourissa peltata,* although I found it to be more abundant in localized areas. Family dominance for Monimiaceae in this habitat was 2.04% of the total individuals (Table 4), somewhat less than at Macabé but still a significant element of the woody flora (Vaughan & Wiehe, 1941).

Areas lying to the west of the central plateau, i.e., the western escarpment and lowland areas in the rain shadow (1,000–1,600 mm precipitation), experience a distinct dry season and support a semideciduous dry forest of Mauritius Ebony (*Diospyros tessellaria* Poir.), *Mimusops,* and *Elaeodendron* (Celastraceae). Of the island's ten species of *Tambourissa,* only *T. quadrifida* occupies this habitat to which it is restricted, e.g., at Yemen Valley (Table 3). The species occurs here as a mid stratum or canopy tree often forming small, localized populations.

Although many Monimiaceae readily sprout sucker shoots from cut stumps, no species were found to occur in secondary forests. Furthermore, regeneration of many is poor or lacking even in indigenous forest highly invaded by vigorous exotic species, suggesting that many should be considered as threatened species. For example, on Mt. Cocotte, which is heavily invaded by numerous exotics, only limited regeneration was observed in *Tambourissa ficus* and *T. peltata,* two of the commonest species. No signs of recent regeneration, however, were apparent in the rare and localized *T. cocottensis* and *T. tetragona.* However, vigorous regeneration of both *Tambourissa peltata* and *T. tau* was observed at Perrier Nature Reserve, which has been kept free of exotics for the last decade by a stringent weeding program carried out by the Forestry Department.

In summary, on one hand, Mauritius has favored the greatest adaptive radiation in *Tambourissa* of any of the satellite islands around Madagascar, probably as a result of its comparatively greater age coupled with the availability of a range of suitable habitats. *Monimia,* on the other hand, is represented by a single species confined to the island's few patches of cloud forest. Its poor representation may be attributable to a lack of suitable habitats or a relatively recent introduction.

RODRIGUES

Rodrigues, the smallest, most isolated, and possibly youngest of the Mascarene islands, only attains ca. 400 m maximum elevation and is the least diverse ecologically. As a result of its extreme isolation and paucity of suitable habitats, Monimiaceae appear to be absent from the island (e.g., Balfour, 1879; Wiehe, 1949; J. Guého, pers. comm.). A single collection of *Monimia ovalifolia* supposedly from Rodrigues is probably wrongly labelled (see discussion under the genus *Monimia*).

COMORE ARCHIPELAGO

The Comores are poorly known botanically but appear to harbor predominantly African and Madagascan floristic elements (Voeltzkow, 1917). Of the four islands, information is available only for Grande Comore (Legris, 1969) in the form of a survey of vegetation types and enumeration of their most common and conspicuous elements.

GRANDE COMORE

Grande Comore, youngest of the islands, has virtually no intact lowland forest remaining. Areas of well-developed lower montane wet and montane cloud forest still remain on the lower windward and mid altitude slopes beginning at ca. 500–800 m, however, notably on the Karthala volcano and La Grille massifs where annual precipitation ranges from ca. 3,000 to 5,000 mm (Legris, 1969). Of recent volcanic origin, the La Grille massif supports mature wet forest dominated by large individuals of *Weinmannia, Anthocleista, Eugenia,* and *Macaranga* attaining ca. 20–30 m, and also harbors the island's only species of Monimiaceae, *Tambourissa comorensis.* One of the largest members of the genus, it appears to be restricted to La Grille where it constitutes an important element of the forest, conspicuous because of its numerous large, brown cupuliform fruits hanging from the trunk and major branches (Fig. 17B).

Wet forest on the Karthala volcano massif is dominated by *Ocotea, Nuxia, Olea,* and *Aphloia,* but no Monimiaceae have been noted or collected there to my knowledge. A cloud zone often forms above ca. 1,000 m. At ca. 1,800–2,000 m the wet/cloud forest zone on Karthala gives way to an ericoid heath formation of *Philippia* similar to that in Madagascar and Réunion; no Monimiaceae are known from this zone.

The leeward western region of the island probably once supported dry forest, of which huge baobabs (*Adansonia digitata* L.) and other scattered trees are the only remnants. No Monimiaceae are known from this zone either.

ANJOUAN

Unfortunately, I was unable to visit Anjouan, which is extremely poorly known botanically. Most of its lowland forest has been destroyed, although the mountainous central massifs (e.g., N'Tingui) support fairly extensive areas of wet and cloud forest due to their rugged relief (I. Tattersall, pers. comm.). Two species of *Tambourissa, T. kirkii* and *T. paradoxa* (syn. *T. johannae*) are known from Anjouan, but little is known of their ecology and distribution. Both apparently occur in the wet and cloud forest zones (Fig. 35). Although Anjouan only attains ca. 1,600 m, it may harbor small amounts of heath vegetation on its highest peaks. Dry forest probably occurred on its dry, lower leeward slopes as is the case for Mayotte and Grande Comore.

MOHÉLI

Mohéli, smallest of the Comores, is also virtually unknown botanically. Although I was unable to visit it, I. Tattersall (pers. comm.) stated that several extensive areas of montane wet forest still remain on its central ridge at Mt. St. Antonio, and between Fomboni and Drondoni (ca. 500–700 m elevation). Collections from these areas made by L. Bernardi in 1967 have revealed the presence of a new endemic species of *Tambourissa, T. moheliensis,* and apparently the only one to occur there. Little is known of its distribution and ecology (Fig. 35). Most of Mohéli's lowland vegetation is now gone. Presumably wet forest occurred on the windward slopes and dry forest on the lower slopes in the rain shadow, as is the case for Mayotte and Grande Comore.

MAYOTTE

Oldest and lowest of the Comores, Mayotte supports only a few small areas of indigenous forest, the rest being cultivated or secondary in nature. Several of the island's highest mountain massifs, i.e., Benara (650 m) and Hachiroungou (500 m), support wet forest dominated by *Nuxia, Aphloia,* and *Macaranga* similar to that found on Grande Comore. Occasional local populations of the Mayotte's only Monimiaceae species, *Tambourissa leptophylla,* still occur here (Fig. 35). A number of large mature individuals and signs of recent regeneration were observed on Benara. *Tambourissa leptophylla* also occurs sporadically as a remnant in wet lowland secondary forest at Barakani and Sada. In the dry, western leeward region remnants of dry forest with *Adansonia digitata* occur on isolated peaks and offshore islets. No Monimiaceae were found to occur there.

In essence, although each of the Comores supports its own single endemic species of *Tambourissa* (two in Anjouan), adaptive radiation of the genus here has been less extensive than in the Mascarenes or Madagascar. As habitat diversity in the Comores is roughly comparable to that in the Mascarenes in spite of their smaller average size, the low *Tambourissa* species diversity may be due to the islands' relative youth or possibly a more recent date of introduction of the genus. That four of the five Comorean species appear to be closely related, and that all species for which data are available are restricted to the wet/cloud forest zone (none are adapted to either dry forest or heath formation), suggests a relatively short history for *Tambourissa* in the Comores.

This review of the ecology and distribution of the Monimiaceae in the Malagasy region demonstrates that members of the family are floristically important constituents of the islands' plant formations. Furthermore, the various species have different life forms ranging from shrubs or understory treelets to mid stratum or even canopy trees. The family attains its greatest diversity and abundance in the lower montane wet and montane cloud forest zones, although a significant number of species are adapted to the lowland wet forest zone. Only a few species are adapted to the high altitude heath formation and the semideciduous dry forest, however. Although many species of *Tambourissa* have the ability to form coppice shoots from cut trunks, they are virtually absent from secondary vegetation and exhibit a poor ability to regenerate when competing with vigorous, invasive exotic species.

MORPHOLOGY AND ANATOMY

Because they are generally considered to be a key family for the critical interpretation of a number of other Lauralean families (e.g., Chloranthaceae, Gomortegaceae, Hernandiaceae, and Lauraceae), the Monimiaceae have been relatively well studied morphologically and anatomically (Baillon, 1871; Hobein, 1889; Perkins, 1898, 1925; Perkins & Gilg, 1901; Metay, 1921; Garratt, 1934; Money et al., 1950; Lemesle & Prichard, 1954; Sampson, 1969a, 1969b, 1969c; Endress, 1972, 1980a, 1980b). However, apart from a few species in the genera *Monimia, Tambourissa,* and to a lesser degree *Decarydendron,* the species in the Malagasy area have not been well studied morphologically or anatomically.

METHODS AND MATERIALS

Gross morphological observations were made from herbarium specimens and collections preserved in alcohol. For venation studies, dried leaves were rehydrated, cleared in KOH, bleached, stained in safranin, dehydrated, and mounted in Permount resin between glass plates according to the method of Dilcher (1974). Prints of venation patterns were made using a photographic enlarger and standard photographic print paper (f3, f4, or f5). Leaf trichomes were prepared for the SEM by Au-Pd sputter-coating and photographs were taken on a Cambridge Stereoscan Mark II. Material for floral anatomical studies was fixed in alcohol or FAA (*Monimia,* most *Tambourissa*), or dried herbarium material was restored in 5% NaOH (*Decarydendron, Ephippiandra*) after which it was dehydrated in a TBA series, embedded in Paraplast, sectioned on a rotary microtome, dewaxed and stained with safranin and fast green, and mounted according to methods in Jensen (1962). In some cases, carpels were cleared in KOH, stained, dehydrated, and mounted in Permount to observe the vasculation.

HABIT AND BARK

Monimiaceae in the Malagasy region are mostly understory to mid stratum treelets or small trees, or large canopy trees. I know of no species that occur as emergents. The shrubby habit is quite rare, and no true vines are known from the region. The boles of all species I have observed were cylindric, often with knobby meristematic swellings in the cauliflorous species. The trunk is basally swollen in *Tambourissa ficus, Tambourissa longicarpa,* and *Decarydendron perrieri,* where the flowers are generally produced. None of the species are known to have buttresses or prop roots.

Species of *Monimia* are small- to moderate-sized mid stratum or canopy trees, often shrubby when growing in exposed habitats. Both *M. amplexicaulis* and *M. rotundifolia* reach ca. 10 m tall, whereas *M. ovalifolia* is known to attain 15 m. Trunks of old individuals of all three species are often somewhat reclining and may reach diameters of 30–40 cm in *M. amplexicaulis* and *M. ovalifolia,* and up to 60 cm in *M. rotundifolia.* The bark is generally pale brown or reddish brown, soft, smooth, and flakes off in patches. Because the species are confined to very humid habitats, the bark is often overgrown with bryophytes and other epiphytes.

Of the Madagascan endemic genera, *Decarydendron* and *Ephippiandra* are shrubs, treelets or trees to 10–25 m tall (e.g., *E. madagascariensis* and *E. tsaratanensis*). No information is available on the boles or bark of these two genera.

Tambourissa includes species with a wide range of woody life forms ranging from shrubs rarely exceeding a meter (*T. cordifolia*) to large canopy trees 10–20 m tall (e.g., *T. comorensis, T. sieberi*). The majority of species, however, are understory treelets (e.g., *T. amplifolia, T. tau*) or small mid stratum trees (e.g., *T. ficus, T. purpurea*). The only reportedly vining species is *T. madagascariensis,* a "lianescent shrub" (*Rababoto sub RN 6028,* P), which may also be a large tree 15 m tall (*Anon. sub herb. Alaotra 2126,* MAD). Except for the shrubby *T. cordifolia,* most species are monocaulescent, although many are capable of forming multiple stems from coppice shoots (e.g., *T. cocottensis, T. tau, T. quadrifida*), after death of the main stem.

Although often licheniferous or covered with bryophytes, the bark of most species of *Tambourissa* is pale grayish or brownish, soft and corky, smooth to longitudinally fissured, and flakes or peels off in strips or patches. For the 16 species examined, characteristics of the slash (an oblique cut through the outer and inner bark) include a beige or pale pink to salmon-colored inner bark (phloem), and whitish or straw colored wood (xylem), both showing the conspicuous wide rays characteristic of many Monimiaceae. No sap or exudate was apparent.

In summary, the Malagasy area Monimiaceae are treelets or trees most abundant in the canopy and lower strata of tropical forests. Only a small number of species have shrubby or lianescent habits. The bark of *Monimia* and many species of *Tambourissa* is relatively uniform, but needs further study in *Decarydendron* and *Ephippiandra.*

WOOD ANATOMY

Anatomical studies of the wood of representative genera and subfamilies of Monimiaceae conducted by Garratt (1934), Money et al. (1950), and Lemesle and Prichard (1954) reveal a number of trends of specialization. Most striking are progressive changes in the vessel members which include a shortening and broadening, a decrease in the degree of end wall overlapping, and a transition from scalariform to simple perforation plates.

Of the four genera examined from the Malagasy area (Money et al., 1950), *Decarydendron, Ephippiandra* (as *Hedycaryopsis*), and *Tambourissa* (all Mollinedioideae sensu Thorne) possess wood anatomical features interpreted as being relatively unspecialized within the family. These include long, thin-walled vessel members with angular, extensively overlapping end walls, and in *Tambourissa* (the only genus for which mature wood was available) scalariform perforation plates (Garratt, 1934; Money et al., 1950).

The xylem of *Monimia* (Monimioideae sensu Thorne) exhibits a number of trends that have been interpreted as advanced within the family (Money et al., 1950). Vessel members of *M. ovalifolia* are relatively short with somewhat obtuse end walls that do not overlap extensively and have perforation plates transitional between scalariform and simple porous. In this respect, specialization in the xylem of *Monimia* (and also *Palmeria*—Mollinedioideae) has attained a level comparable to that of *Peumus* (also Monimioideae), also with simple perforation plates.

Common wood anatomical features shared by both the Monimioideae and the Mollinedioideae are: scanty wood parenchyma; rather broad, multiseriate rays; presence of septate fibers; presence of fibers and hippocrepiform sclerids in the stem pericycle (Money et al., 1950).

STEMS AND PHYLLOTAXY

Adult phyllotaxy in *Monimia, Decarydendron, Ephippiandra,* and most species of *Tambourissa* is opposite to subopposite and decussate. The three *Tambourissa* species in species Group 8 have ternate to subalternate adult leaves (Table 1), although seedlings of two, *T. ficus* and *T. peltata,* have opposite decussate leaves. On the other hand, adult leaves of species which are normally opposite are sometimes ternate on vigorous sucker shoots (e.g., *Monimia ovalifolia, Tambourissa purpurea,* and *T. pedicellata*). Although opposite and decussate, the adult leaves of *T. tau* (Fig. 39A) are unique in being clustered into pseudoverticels of two to four pairs, separated by long "internodes." Phyllotaxy is generally a constant, species-specific feature.

Leafy stems of most species of all four genera are more or less terete with flattened, somewhat dialated nodes. *Tambourissa tetragona* is unique in having winged, quadrangular stems, whereas those of the ternate leaved species (Group 8) are somewhat trigonous.

Stems of *Decarydendron, Ephippiandra,* and most *Tambourissa* species bear sparse to dense, straight or undulate, simple or rarely fasciculate (e.g., *T. comorensis, T. mohelensis*) lignified trichomes. In a few species even the new growth is virtually glabrous (e.g., *T. cocottensis, T. cordifolia,* and *T. tetragona*). In *Monimia,* the stems are scabrous to velutinous with an indument of stellate, fasciculate and simple trichomes. Lenticels often occur on the stems of certain species (e.g., *T. ficus, T. peltata, E. perrieri, E. domatiata,* and *E. myrtoidea*) but are absent in most. Stem characters thus provide a number of species-specific, taxonomically useful features.

Monimia, Decarydendron, Ephippiandra, and *Tambourissa* all characteristically possess multiple axillary buds of which I found no mention in the literature. In all three species of *Monimia* (as in *Peumus*), three horizontally oriented buds are usually present in each leaf axil, the central one being largest and developing first (if at all). The vegetative buds have small, pubescent scales, whereas those enclosing the inflorescence are large, brown, and subglabrous. In the remaining genera, all Mollinedioideae, the buds are oriented longitudinally in the leaf axil, the central one usually being largest and the first to develop (if at all). On flowering branches of the ramiflorous species *E. madagascariensis* and *E. tsaratanensis* there are three to five buds, the central one usually giving rise to the inflorescence and the lateral ones to vegetative shoots. In *D. helenae* var. *stenophyllum* the buds occur in groups of three, whereas in *E. microphylla* and *E. myrtoid-*

ea they are solitary or in pairs. Three, less commonly two, axillary buds are present in nearly all species of *Tambourissa* examined, regardless of whether the inflorescence is terminal, ramiflorous or cauliflorous. On flowering stems of ramiflorous species such as *T. purpurea,* the large central bud frequently but not invariably gives rise to the inflorescence. On vegetative stems, the central bud usually develops first, although two buds may occasionally develop into vegetative shoots simultaneously. *Tambourissa tetragona* is exceptional in that only one bud is obvious. However, vigorous sucker shoots of *T. ficus* may produce up to six buds extending in a row for several centimeters above the leaf axil (*Lorence 2235,* MO).

LEAVES

The terminology used to describe leaves in this monograph follows Hickey (1973, 1977), Hickey and Wolfe (1975), and to an extent Lawrence (1951). Leaves of all Monimiaceae are exstipulate, considered by Hickey and Wolfe (1975) to be an advanced condition within the Laurales. Characters of the petiole and lamina, including size and shape, margin, venation, and pubescence, provide a series of taxonomically useful features in many taxa.

Petiole. The leaves of most genera and species have a well-differentiated lamina and petiole, but *Monimia amplexicaulis* (Fig. 4A) and *Tambourissa cordifolia* (Fig. 8B) are unique in having sessile cordate, amplexicaul leaves. Petioles of most other species are slender to stout, of variable length but much shorter than the lamina, and are adaxially flattened or canaliculate. They are either glabrous or bear an indument of trichomes similar in type and density to that of the stem internodes. In all three species of *Monimia* (*M. amplexicaulis, Lorence 2503,* MO; *M. ovalifolia, Lorence 1857,* MO; *M. rotundifolia, Lorence 2472,* MO), the vascular strands of the petiole are united into an adaxially flattened cylinder (see also Money et al., 1950). In the other genera which I examined (*Ephippiandra myrtoidea, Baron 1355,* K; *E. madagascariensis, Bernardi 11977,* MO), and six species of *Tambourissa* (*T. cocottensis, Lorence 2287,* MO; *T. crassa, Lorence 2767,* MO; *T. elliptica* subsp. *micrantha, Lorence 2488,* MO; *T. ficus, Lorence 2162,* MO; *T. pedicellata, Lorence 2385,* MO; and *T. tetragona, Lorence 2286,* MO), the petiolar vascular strands are aggregated into a shallow, U-shaped arc. This corresponds with Metay's (1921) findings for *T. floricostata* (as *Schrameckia madagascariensis*) and *T. thouvenotii.*

Lamina. Leaves of *Monimia* are subcoriaceous to coriaceous, usually ovate to elliptic or suborbiculate, and their size and shape are generally much more polymorphic in *M. ovalifolia* and *M. rotundifolia* than in *M. amplexicaulis.* Although the extreme forms appear to be very distinct (Fig. 4), leaf size and shape in *Monimia* do not provide stable taxonomic features. Likewise, shape of the apex is quite variable (acuminate, acute, or obtuse) and of little taxonomic importance in all three species. Characters of the leaf base, however, are useful in distinguishing *M. amplexicaulis,* where it is deeply cordate and amplexicaul, from the other two species where it ranges from shallowly cordate to rounded, obtuse, acute or decurrent (Fig. 4).

Leaves of the three species of *Decarydendron* do not differ markedly from each other, ranging from elliptic to oblong or obovate. The texture is chartaceous to subcoriaceous, the apex acute or acuminate, and the base cuneate.

Leaves of the six species of *Ephippiandra* are small- to medium-sized and chartaceous to coriaceous in texture. Laminar shape is generally characteristic for each species: ovate or elliptic with acute or acuminate apices and cuneate to rounded bases in *E. microphylla* and *E. myrtoidea* (Fig. 6A); elliptic with a retuse apex folded downward into a flap in *E. perrieri* (Fig. 6B); obovate-elliptic to rhombic and apiculate in *E. domatiata*; orbicular with an obtuse to truncate base and obtuse to rounded apex in *E. madagascariensis* and *E. tsaratanensis.* (Fig. 6E, F).

The 43 species of *Tambourissa* display a wide array of leaf morphologies which are relatively constant and species-specific. In widespread species with a broad ecological amplitude (e.g., *T. peltata, T. purpurea*), considerable intraspecific variation occurs in size and shape, generally between populations growing in different habitats. Texture ranges from membranaceous in *T. leptophylla* to coriaceous in *T. parvifolia* and *T. religiosa.* Size varies from small in *T. parvifolia* (attaining only 47 mm by 22 mm) which grows in high altitude montane forest, to very large in *T. amplifolia* (attaining 500 mm by 240 mm) which grows in lowland wet forest. Leaf shape varies considerably within many species but in others it is of considerable taxonomic significance, e.g., in distinguishing the two subspecies of *T. elliptica.* Leaf shape in the genus ranges

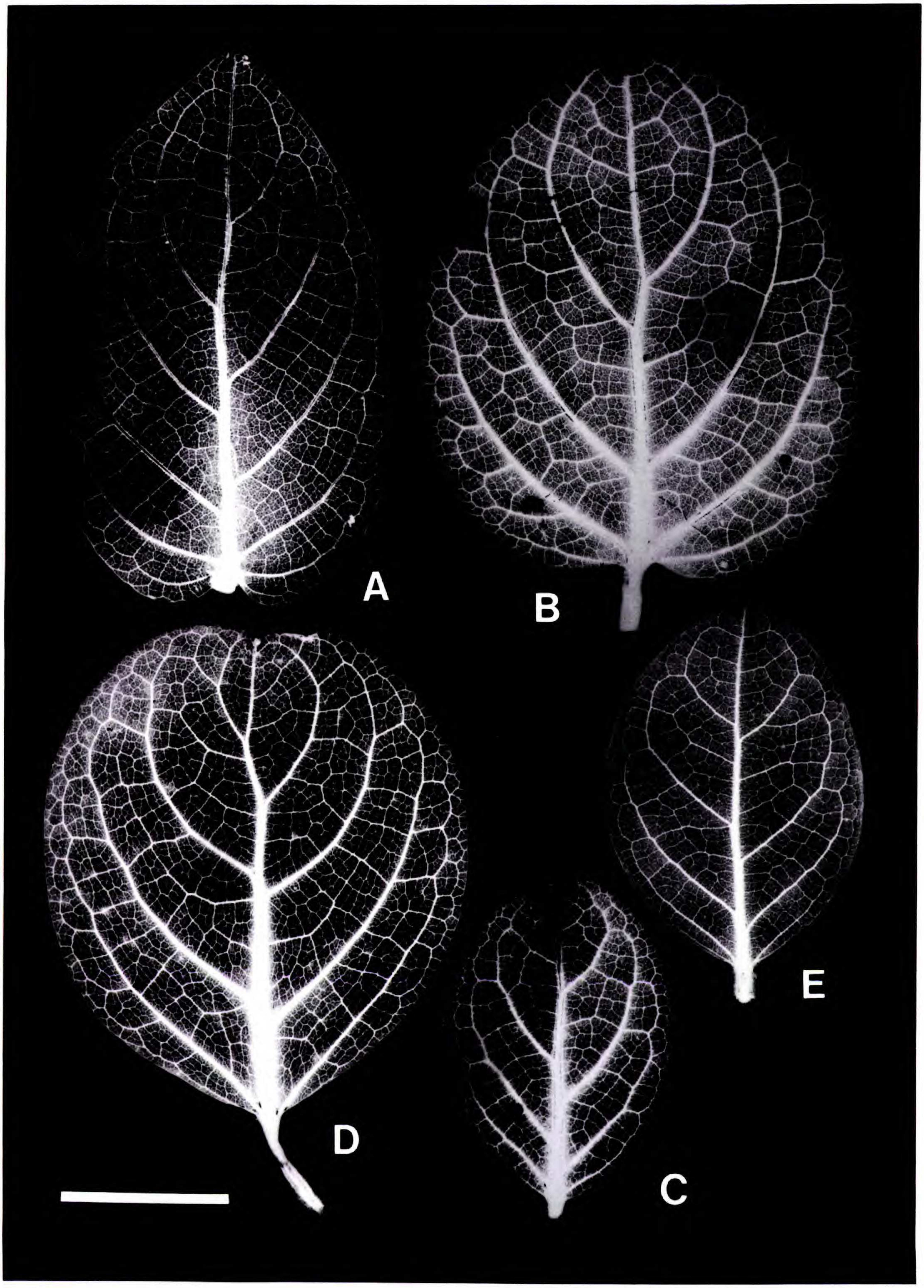


FIGURE 4. Leaf clearings of *Monimia.*—A. *M. amplexicaulis, Rivals s.n.* (TL-R).—B. *M. rotundifolia, Rivals s.n. in June 1943* (TL-R).—C. *M. rotundifolia, Bosser 21332* (P).—D. *M. ovalifolia, Cordemoy s.n.* (TL-R).—E. *M. ovalifolia, Guého sub MAU 14130* (MAU). Bar equals 25 mm.

from cordate or ovate to elliptic, oblong, or obovate.

Studies of leaf anatomy in *Monimia* and *Tambourissa* (Hobein, 1889; Metay, 1921) show their laminar structure to be similar to that of many bifacial dicot leaves. The two species of *Monimia* and six species of *Tambourissa* examined by them all have a cuticle, an upper epidermis, a hypodermis consisting of one to six cell layers, a mesophyll differentiated into a palisade layer one or two cells thick and a spongy layer many cells thick, and a lower epidermis also covered by a cuticle. Stomata are restricted to the lower epidermis in all species except *T. thouvenotii,* which also has stomata in the upper epidermis (Metay, 1921).

Leaves of Monimiaceae are characterized by the presence of spheroid laminar glands or secretory cells containing so-called "ethereal" oils which impart a particular odor to many species. In most species of *Tambourissa* these are concentrated in the mesophyll, but lesser numbers also occur in the lower epidermis and hypodermis (Hobein, 1889; Metay, 1921). Hobein (1889) stated that both *Monimia ovalifolia* and *M. rotundifolia* have secretory cells restricted to the hypodermis and not in the mesophyll as in *Tambourissa* and the other genera he studied. My investigations of hand sectioned, alcohol fixed leaves show that secretory cells are restricted to the hypodermis only in *M. ovalifolia,* both in plants from Mauritius (*Lorence 1857, 2896,* MO) and from Réunion (*Lorence 2757,* MO). In *M. amplexicaulis* (*Lorence 2503,* MO) and *M. rotundifolia* (*Lorence 2472,* MO), secretory cells were found to occur not only in the hypodermis, but also in the interface between the palisades and spongy mesophyll. An examination of sections of restored leaves of *Decarydendron helenae* var. *stenophyllum* (*Humbert 6613,* K), *Ephippiandra tsaratanensis* (*Gentry 11605,* MO), and *E. myrtoidea* (*Baron 1263,* K) shows that they are fundamentally similar to species of *Tambourissa* anatomically.

Venation and margin. The Monimiaceae possess several distinctive trends which Hickey and Wolfe (1975) consider to be advanced within the Laurales, notably development of the Monimioid tooth with an unbraced medial vein and an indurated cap, and secondary veins originating at uniform angles to the costa.

All three species of *Monimia* possess stoutly brochidodromous venation of the festooned type characteristic of the family. Three to four pairs of secondary veins originate at comparatively uniform angles, are bowed to geniculate, follow a regular, slightly sinuous course and delimit relatively regular and uniform intercostal areas (Fig. 4A–E). Consequently, all three species fall into Hickey's (1977) second rank leaf category. Distally the secondaries continue to form another, higher order of loops characteristic of the festooned brochidodromous venation pattern (Hickey & Wolfe, 1975). The numerous intermarginal loops of the last order unite to form a weak, fimbriate intramarginal vein generally lacking in the other genera.

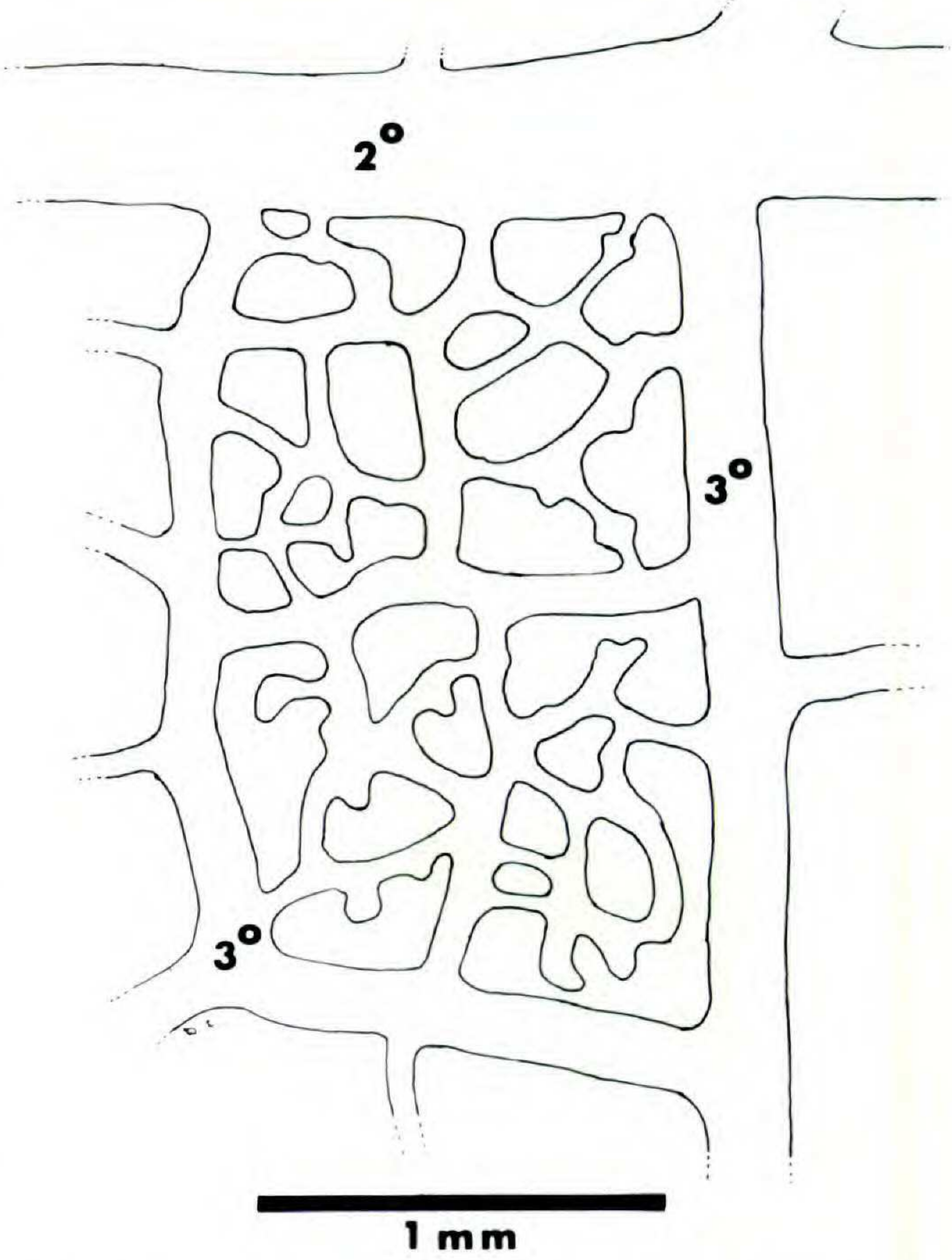


FIGURE 5. Camera lucida drawing of ultimate venation in cleared leaf of *Monimia ovalifolia, Bijoux sub MAU 1310* (MAU). 2° = secondary venation, 3° = tertiary venation.

Intercostally, the tertiary veins originate at right angles from the secondaries and their arches and unite to form a series of strong, transverse tertiaries which in turn ramify at right angles and then anastomose admedially to form composite intersecondaries that usually follow a zig-zag course. These tertiary areoles are generally orthogonal (rectangular or pentagonal) and much more regular than in the other genera (Figs. 4, 5). The quaternaries arise from the tertiaries at nearly right angles to form fairly regular rectangular areoles. Vein orders above the quaternary are generally indistinct and ramify to form a reticulum of irregular areoles with included veinlets that anastomose or remain free (Fig. 5). Terminal idioblasts appear to be absent from the veinlets. The number and pattern of veins in *Monimia* provide few characters useful in separating the species, although they are characteristic of the genus as a whole.

Adult leaves of all three *Monimia* species have entire, generally slightly revolute margins. Seedling leaves of *M. ovalifolia* and *M. rotundifolia* (unknown in *M. amplexicaulis*) are also entire, as opposed to those of *Tambourissa* (D. Lorence, pers. observ.) and *Hortonia* (Endress, 1980a) which are generally dentate. Although the Monimioid tooth is, ironically, absent in *Monimia*, its venation is highly organized and appears to be advanced in this respect. The genus may possibly have undergone loss of teeth secondarily, as appears to be the case for *Tambourissa*.

Venation in all three species of *Decarydendron* is festooned brochidodromous. The six to 12 pairs of secondaries arise at quite constant angles, delimit regular intercostal areas, and continue to loop for several orders. Tertiary veins arising inside the secondary arches ramify admedially to form a reticulum of irregular areoles as they descend obliquely across the intercostal area. The quaternaries arise from the tertiaries at irregular angles and delimit irregular areoles. Vein orders above the quaternary are indistinct, and probably ramify to form free, included veinlets. Adult leaves of all three species of *Decarydendron* are serrate-dentate along the greater portion of their plane margins, each tooth ending in an indurated cap. An unbranched distal excurrent vein arising from the outer series of brochidodromous arches runs directly into each tooth. In this respect the venation is not truly semicraspedodromous according to Hickey's (1973) definition.

Species of the genus *Ephippiandra* (including *Hedycaryopsis*) display a distinctive trend from festooned brochidodromous to specialized and highly organized semicraspedodromous and craspedodromous patterns, the latter unknown elsewhere in the family. Leaves of *E. microphylla, E. myrtoidea,* and *E. perrieri* are small with only four to six pairs of secondary veins which unite into arches near the margin, and the festooning is often weak (Fig. 6A, B). Several tertiary veins arise on the distal parts of the secondary arches and descend parallel to the secondaries or somewhat obliquely across the intercostal areas, often ramifying into strongly admedial branches as they approach the costa. The tertiaries delimit irregular intercostal areas in *E. myrtoidea,* but these are more regular and orthogonal in *E. perrieri.* Higher vein orders above the tertiary are not very distinct and generally form a more or less random reticulum of irregular areoles, ultimately terminating in free, dendroid veinlets lacking idioblasts. Margins are entire and somewhat revolute in *E. myrtoidea* and *E. perrieri,* but those of *E. microphylla* generally have a single pair of small teeth in the apical portion arising from exmedial branches of the secondary arches.

Leaves of *E. domatiata* (Fig. 6C, D) are likewise small with two to three pairs of secondaries, but show certain modifications towards the semicraspedodromous pattern. Although the weak basal pair of secondary veins forms a series of festooned loops in the customary brochidodromous manner, the second, stronger pair ascends for over half the lamina's length before joining the next pair above. On each side of the lamina one of the secondary branches runs directly into the margin, terminating in a small tooth. The tertiaries delimit fairly irregular intercostal areas, although the quaternaries form more regular areoles with free, branching veinlets. The margin is moderately revolute, and it is the only species known to have barbate domatia in the basal secondary vein axils, hence the specific epithet.

Ephippiandra tsaratanensis (Fig. 6E) has much larger, broader leaves which show a weakening of the brochidodromous pattern and the formation of sunken marginal teeth. As each of the four to seven pairs of secondary veins bifurcates, each branch generally unites with an adjacent branch to form a weak arch whose exmedial portion in turn gives rise to one or more distal branches. Each of these runs to the margin where it terminates in a rounded, centrally depressed tooth. The intersecondary webbing pattern of the tertiaries is stronger than in the preceding species, with more regular orthogonal, often quadrangular, tertiary areoles frequently bisected by zigzagging admedial branches. The quaternaries form generally small, more or less orthogonal areoles with free, included branched veinlets.

Leaves of the sixth species, *Ephippiandra madagascariensis* (Fig. 6F) are the most highly specialized of all, being almost orbicular with four to five pairs of secondary veins forming an open, craspedodromous pattern due to a further weakening of the secondary arches. Each secondary departs from the costa at a uniform angle

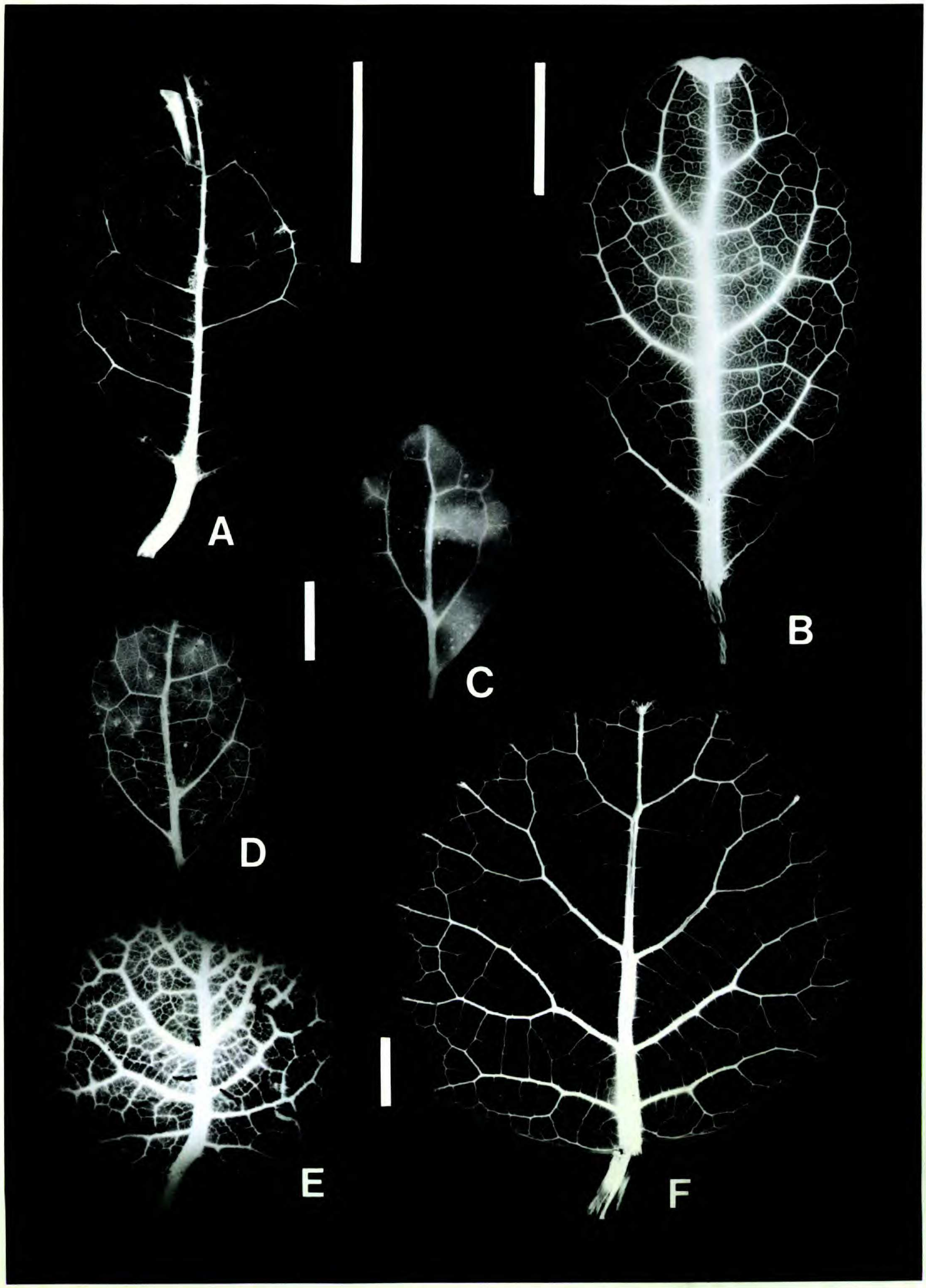


FIGURE 6. Leaf clearing of *Ephippiandra*.—A. *E. myrtoidea, Baron 1355* (K).—B. *E. perrieri, Morat 2332* (MAD).—C, D. *E. domatiata, Capuron 8828-SF* (P).—E. *E. tsaratanensis, Gentry 11605* (MO).—F. *E. madagascariensis, Bernardi 11977* (MO). Bars equal 10 mm.

and generally bifurcates once or rarely twice before the (usually basal) branch terminates in a single, depressed tooth as in the previous species. Occasionally, an apical sub-branch unites with a superadjacent secondary. As in the latter species, the tertiaries form a strong intersecondary cross webbing pattern delimiting regular intercostal areas. The tertiaries nearest the costa frequently display a strongly admedial zigzag branching pattern, whereas the quaternaries generally form irregular areoles with highly branched, free included veinlets as in the other species. The margin of *E. madagascariensis* is sinuate-dentate with seven to nine pairs of sunken teeth, including one at the apex, as in the preceding species. These teeth contain terminal tracheary elements and appear to be hydathodal.

A situation analogous to that in *Ephippiandra* occurs in *Hibbertia* (Dilleniaceae). Rury and Dickison (1977) explain the ontogenetic transitions in *Hibbertia* as follows:

> "The craspedodromous venation pattern appears to be (in most cases) the result of an ontogenetic modification of the weakly brochidodromous pattern. Semicraspedodromous venation apparently resulted from formation and subsequent vascularization of marginal teeth in leaves with weakly brochidodromous venation. The tooth vasculature arises exmedially from the brochidodromous arch in leaves of *Hibbertia cuneiformis*, etc."

This same transition is apparent in the six species of *Ephippiandra*: a weakening and opening of the brochidodromous pattern with subsequent vascularization of the teeth from the secondary branches. This transition from weak brochidodromy to simple craspedodromy could result from a differential thickening of the portion which connects the basal part of the secondary arch with the marginal tooth, which can be seen in the basal veins of *E. madagascariensis*. According to Rury and Dickison (1977), Hickey (pers. comm.) stated that the ontogenetic transition from semicraspedodromy to simple craspedodromy has resulted from such a shift in vein development in many dicot leaves.

Tambourissa species (including *Phanerogonocarpus*) have venation patterns based on the festooned brochidodromous theme. Number of secondary veins ranges from three or four pairs (e.g., *T. parvifolia*, Fig. 8C; *T. elliptica* subsp. *elliptica*, Fig. 7D; *T. thouvenotii*, Fig. 7A), to six to 12 pairs in *T. elliptica* subsp. *micrantha* (Fig. 7E). The secondaries are stout, straight or sinuate, and delimit intercostal areas which may be irregular (*T. thouvenotii*, Fig. 7A), or quite regular (*T. elliptica* subsp. *micrantha*, Fig. 7E; *T. cordifolia*, Fig. 8B). Species with fewer secondary veins frequently have less regular intercostal areas; some of these approach Hickey's (1977) "first rank" leaf category in this respect (e.g., *T. thouvenotii*, Fig. 7A). The majority of species, however, fall into his "second rank" category. In these, the secondaries from a fairly strong series of brochidodromous arches and continue to loop or festoon for several orders. The ultimate exmedial series of loops is often irregular and discontinuous (e.g., *T. leptophylla*, Fig. 8E), and does not form a true marginal fimbrial vein, although the strong intramarginal loops of *T. religiosa* resemble a fimbrial vein (Fig. 8D). The tertiary veins arise at wide acute to slightly obtuse angles from the secondaries and their arches, and are often admedially and obliquely ramified, forming strong, composite intersecondaries (e.g., *T. elliptica* subsp. *micrantha*, Fig. 7E). Tertiary areoles are generally irregular, although orthogonal areoles may be delimited by transverse tertiaries in some species with more highly organized venation (e.g., *T. peltata*, Fig. 8A; *T. elliptica* subsp. *elliptica*, Fig. 7D). Higher order veins are generally indistinct above the quaternary and sometimes tertiary levels. The quaternaries generally ramify and anastomose to form irregular areoles with dendroid, highly branched, free included veinlets. Terminal idioblasts are absent.

The margins of adult leaves of the majority of *Tambourissa* species are entire and plane to revolute. Exceptional are *T. thouvenotii*, *T. trichophylla*, and the two species formerly included in *Phanerogonocarpus*, i.e., *T. alaticarpa* and *T. longicarpa*. The former two possess half-toothed leaves with one to eight pairs of Monimioid teeth in the apical portion of the lamina. In *T. trichophylla* (Fig. 7C), the secondary arches are strong and delimit low, broad intercostal areas, with an excurrency of the secondary arch running into each tooth. The apical portion of the lamina is therefore semicraspedodromous. In *T. thouvenotii* (Fig. 7A), the secondaries delimit high, narrow intercostal areas and the arches are much weaker, approaching the semicraspedodromous pattern of *Ephippiandra*. In some leaves of *T. thouvenotii* the main, apical secondary branch runs directly into the tooth, and any festooning is very weak. In others, it more closely resembles the pattern in *T. trichophylla*.

Leaves of the two species formerly included in *Phanerogonocarpus* (*T. alaticarpa* and *T. lon-*

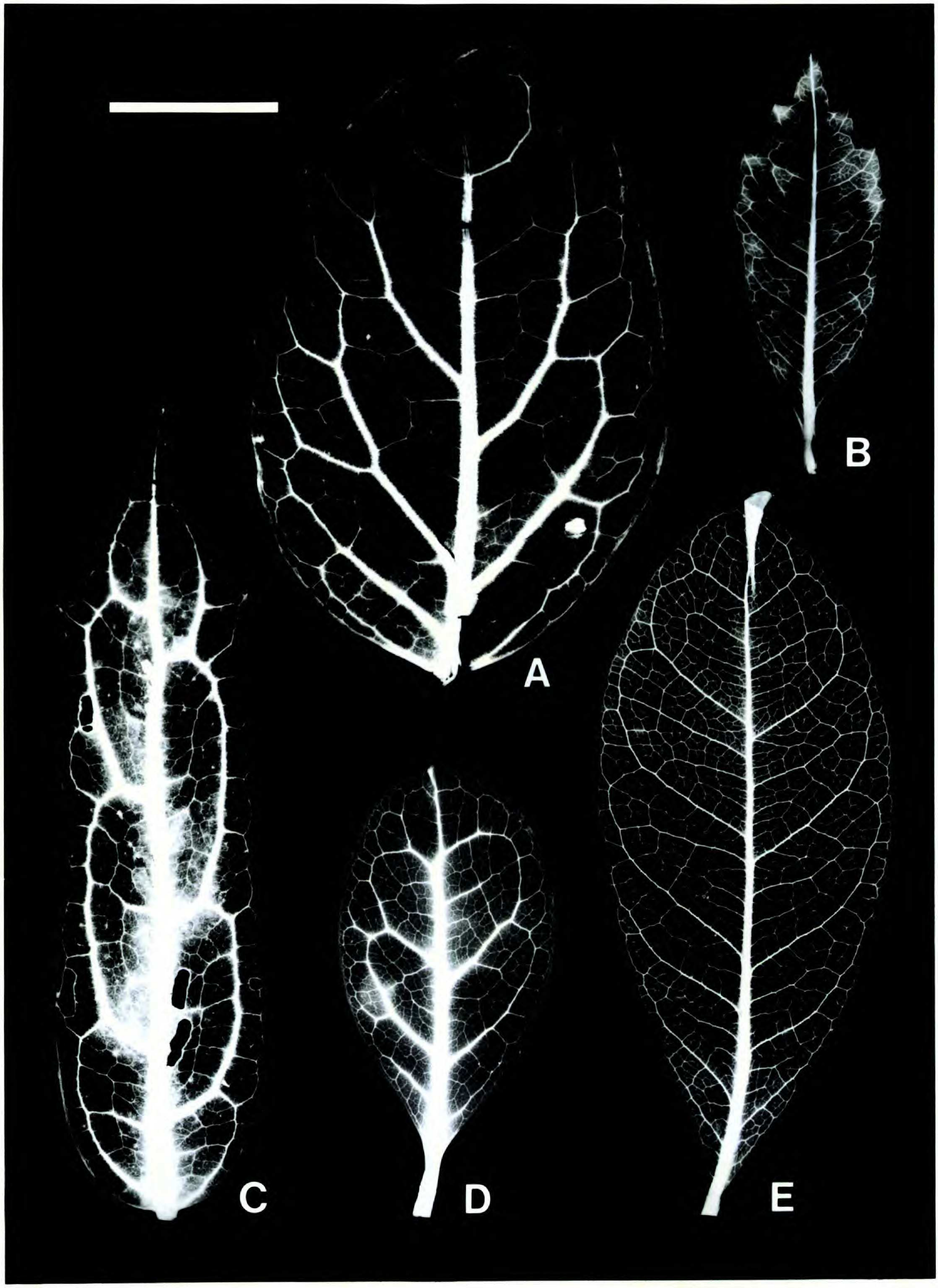


FIGURE 7. Leaf clearings of *Tambourissa*.—A. *T. thouvenotii, Thouvenot s.n. in 1919* (BM).—B. *T. ficus*, juvenile from sucker shoot, *Richardson 4042* (K).—C. *T. trichophylla, Lorence 1879* (MO).—D. *T. elliptica* subsp. *elliptica, Friedmann 2299* (P).—E. *T. elliptica* subsp. *micrantha, Coode 4956* (K). Bar equals 25 mm.

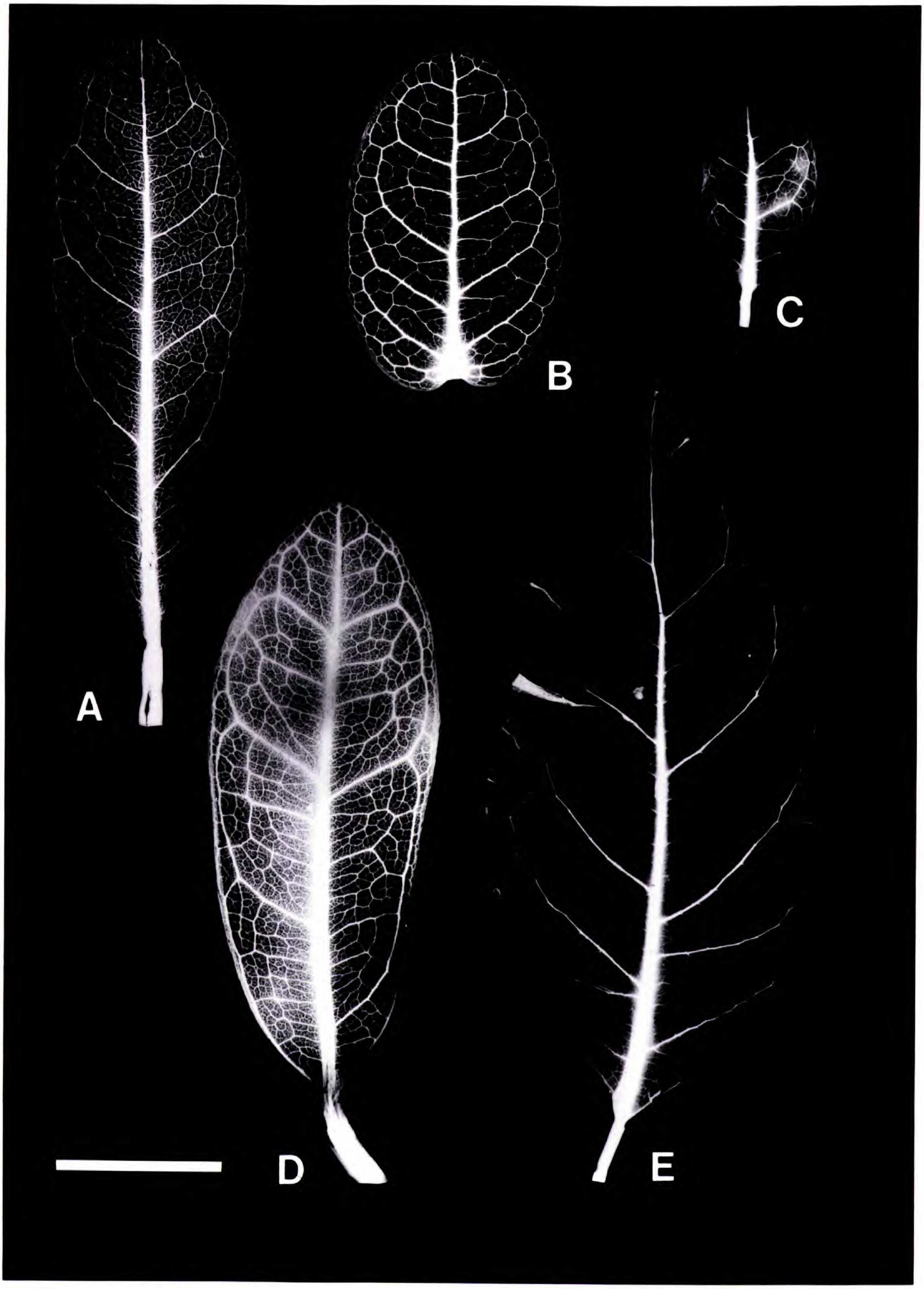


FIGURE 8. Leaf clearings of *Tambourissa*.—A. *T. peltata, Guého sub MAU 12543* (MAU).—B. *T. cordifolia, Lorence M 144* (MO).—C. *T. parvifolia, Baron 4204* (K).—D. *T. religiosa, Decary 6554* (P).—E. *T. leptophylla, Tattersall s.n.* (MO). Bar equals 25 mm.

gicarpa) have five to eight pairs of secondary veins arising at quite uniform angles which delimit fairly regular intercostal areas and unite in a festooned brochidodromous pattern. In *T. alaticarpa,* the apical ⅔–¾ of the margin is dentate with eight to ten pairs of slender, antrorse teeth (Fig. 17A). That of *T. longicarpa* is broadly dentate with two or three pairs of large teeth in the apical ⅓–½ of the lamina. In both, the teeth arise from exmedial branches of the secondary or tertiary arches, thus rendering the venation semicraspedodromous.

In the context of Rury and Dickison's (1977) findings for *Hibbertia* where teeth develop in the adult leaves, it would seem that the dentate species of *Tambourissa* are advanced within the genus. My field studies show, however, that seedlings of virtually all species of *Tambourissa,* which I have seen, produce apically dentate leaves. This condition frequently also occurs on sucker shoots (e.g., *T. ficus,* Fig. 7B) where they are gradually lost in the ontogenetic transition to entire adult leaves. These *Tambourissa* species therefore appear to lose their teeth secondarily, as also occurs in *Hortonia* (Endress, 1980a). In this context, the four dentate species may represent cases of neoteny. This does not, however, contradict Hickey and Wolfe's (1975) suggestion that the Monimoid tooth is an advanced feature within the family.

TRICHOMES

Apart from the three virtually glabrous *Tambourissa* species mentioned above, stems and leaves of most species in all four genera bear at least some trichomes. Leaf pubescence ranges from a few scattered hairs along the petiole and major veins, to the entire lamina being canescent or velutinous-tomentose. Stem pubescence is comparable to that of the leaf. Trichomes of all the genera examined are nonglandular, lignified (e.g., stain pink or red with phloroglucinol; Hobein, 1889), and are simple and unicellular (except in *Monimia*). In a few *Tambourissa* species they are fasciculate, i.e., grouped into clusters of two or three.

Three types of trichomes occur in *Monimia*: long, unicellular; multicellular, fasciculate consisting of two to eight long, ascendent, unicellular arms united basally to form the stalk; short, appressed, multicellular stellate or stellate-peltate composed of six to 16 horizontal arms radiating from a common center and joined basally to form the stalk. Trichome density is greatest on the abaxial laminar surface where they form a thick, whitish indument completely obscuring the leaf surface (Fig. 9E), whereas they are scattered and more easily distinguished on the adaxial surface. Trichomes play a key role in distinguishing the three species of *Monimia. Monimia ovalifolia* is distinct in having small, appressed, stellate-peltate trichomes with six to 16 short arms united basally for ⅓–½ their length (Fig. 9D, E), a character shared by populations both from Mauritius and Réunion. In addition to stellate trichomes with fewer long, free arms, *M. amplexicaulis* and *M. rotundifolia* also have simple and fasciculate trichomes (Fig. 9A–C). Although both the latter species may display considerable variation in trichome composition, even within a single population, they are modally distinct.

In the Mollinedioideae, *Ephippiandra domatiata, E. madagascariensis, E. microphylla, E. myrtoidea,* and *E. perrieri* are all sparsely pubescent or subglabrous with short, pale simple trichomes, whereas *E. tsaratanensis* is easily distinguished by its long, dense simple reddish trichomes. Trichomes of *Decarydendron* are simple, yellowish, and generally longer than in *Ephippiandra.* Leaf pubescence in *Tambourissa* ranges from completely glabrous in a few species (e.g., *T. cocottensis, T. tetragona,* species Group 5), to subglabrous (e.g., *T. tau,* species Group 5), canescent or villous in many (e.g., *T. nosybensis, T. hildebrandtii,* species Group 1B), or even densely velutinous-tomentose in a few (e.g., *T. thouvenotii, T. trichophylla,* species Group 1A; *T. longicarpa,* species Group 8). Trichomes therefore constitute a taxonomically useful character in the Monimiaceae.

INFLORESCENCE

Inflorescence structure in the four genera is quite variable: thyrsic, cymose (pleiochasial, dichasial, or monochasial), fasciculate, or solitary. Although more than one inflorescence type frequently occurs within a given species, and often on a single individual, the inflorescence generally provides a taxonomically useful suite of characters. Flowers of all the genera and species in this study are unisexual, and sexual makeup of the inflorescence is often stable and characteristic. For example, *Monimia* is invariably dioecious, although sex expression in the other taxa is often more variable. Inflorescence position varies greatly within the genera, but is frequently

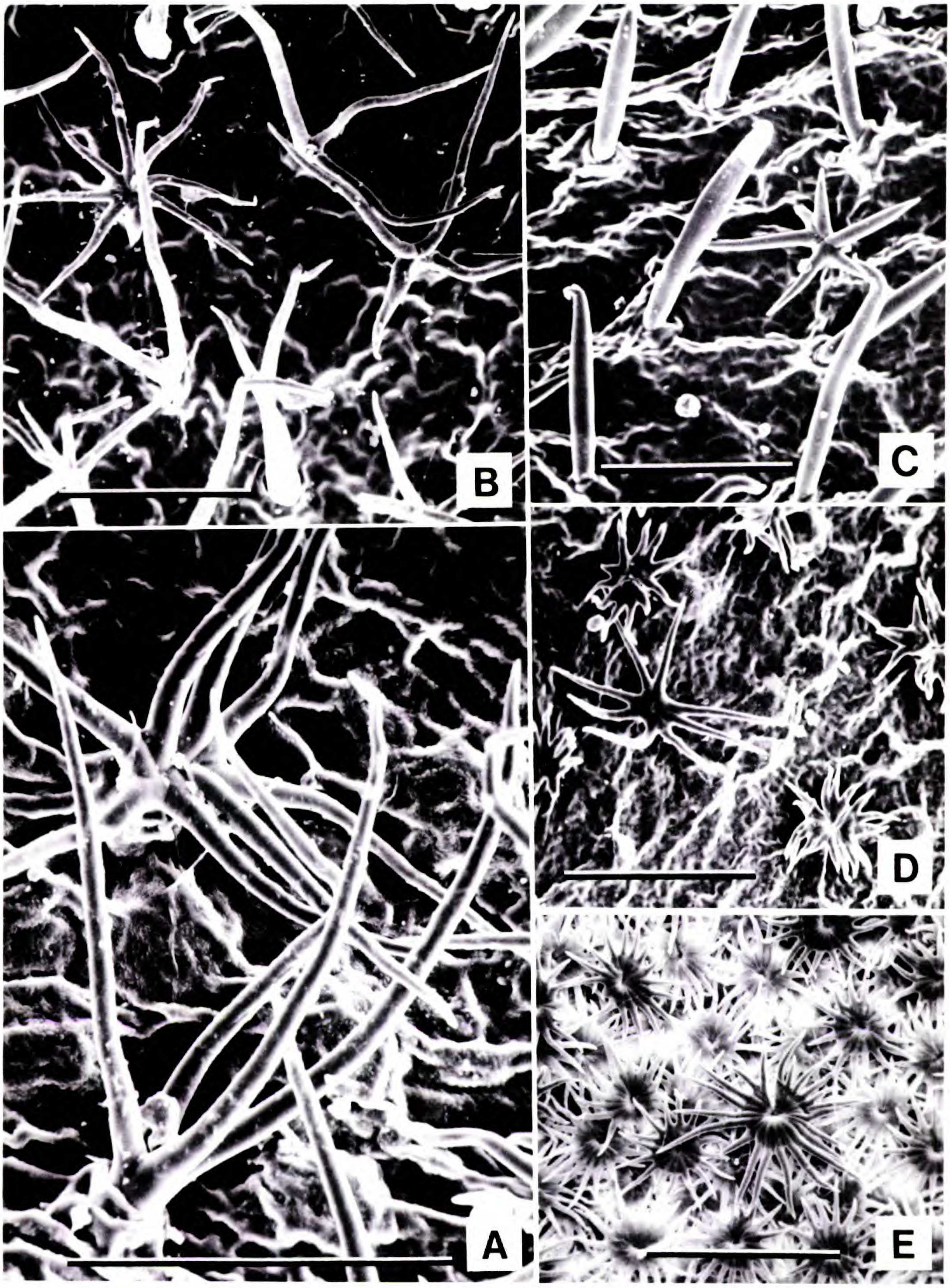


FIGURE 9. Scanning electron micrographs of *Monimia* leaf trichomes.—A. *M. amplexicaulis*, adaxial leaf surface, *Capuron SF-28210* (P).—B. *M. rotundifolia*, adaxial leaf surface, *Friedmann 781* (P).—C. *M. rotundifolia*, adaxial leaf surface, *Bosser 21332* (P).—D. *M. ovalifolia*, adaxial leaf surface, *Guého sub MAU 14097* (MAU).—E. *M. ovalifolia*, abaxial leaf surface, *Friedmann 1884* (P). Bars equal 0.5 mm.

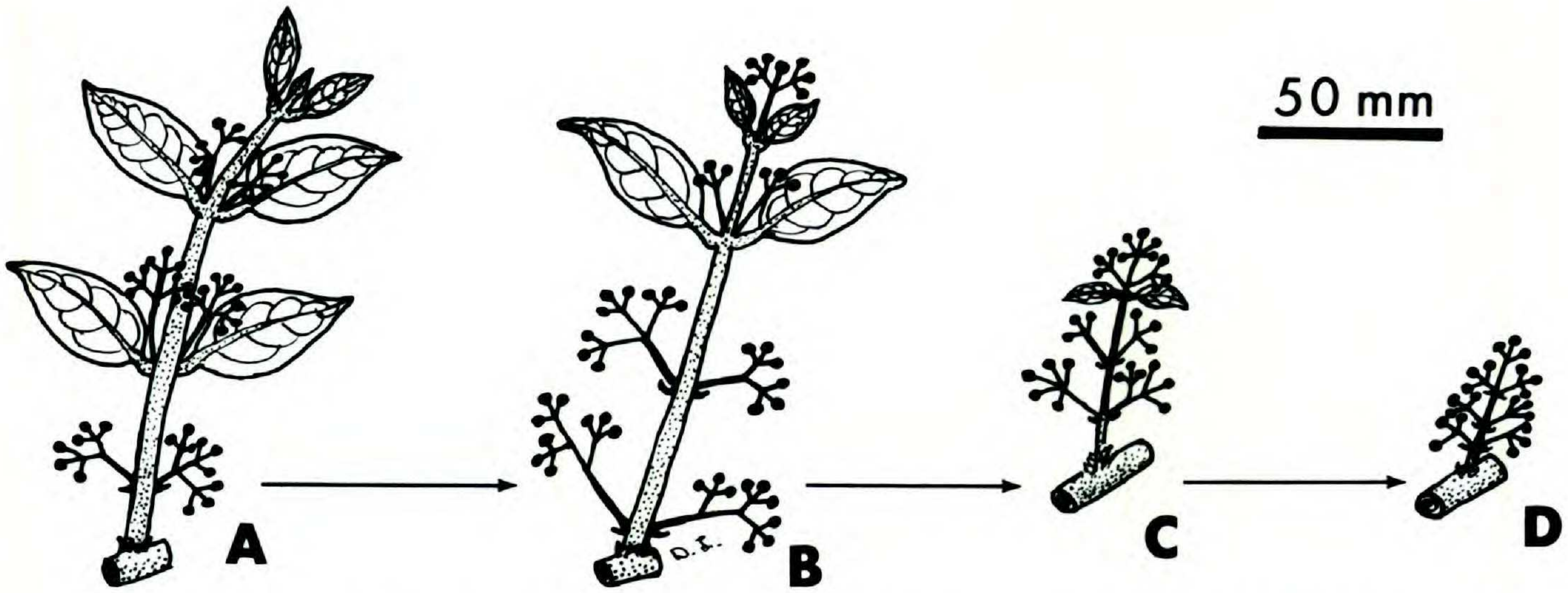


FIGURE 10. *Monimia* inflorescence types, hypothetical reduction series showing derivation of different types. Flowers are depicted as being in one plane, whereas they are actually decussately arranged.—A. Indeterminate leafy shoot with axillary thyrses.—B, C. Determinate leafy thyrses.—D. Thyrse. Bar equals ca. 50 mm.

modally distinct for given species. A brief review of the inflorescence characters will be given for each genus.

Observations on numerous herbarium specimens and living plants reveal that all three species of *Monimia* are dioecious. Inflorescences of all three species are extremely polymorphic and have been variously described as panicles, umbels, racemes (e.g., Baker, 1877), and cymes (Hutchinson, 1964). The ultimate determinate floral unit consists of from two to eight, but usually three, flowers on subequal pedicels attached to a common axis at the same point. As all the flowers in the unit are of the same sex and size, and furthermore all open at about the same time, it does not represent a cyme or pleiochasium in the usual sense (e.g., Lawrence, 1951), but is truly umbelloid. Groups of two to four umbelloid units may be further aggregated or dispersed along a common axis in a thyrse-like manner. The resulting units are borne decussately on a central axis in various ways; up to four different inflorescence types may occur on a given individual, all ramiflorous. These appear to represent a reduction series from an indeterminate leafy shoot with simple axillary thyrses to a leafless, determinate thyrse (Fig. 10A–D).

A) The discrete umbelloid or thyrsic floral units are axillary and occasionally subfoliar on leafless nodes near the basal portion of the actively growing, indeterminate leafy shoot. Each subfoliar unit is subtended by a single caducous, brown bract presumably representing a reduced leaf.

B) The next stage involves the addition of a terminal floral unit. Addition of further lateral units with a concomitant reduction in the number of leaves, which are replaced by bracts, results in the entire structure becoming a determinate leafy thyrse.

C) Further suppression of leaves and shortening of the floral axis results in a more contracted, but still leafy, thyrse.

D) Finally, suppression of all the leaves and their replacement by bracts and still further shortening of the floral axis results in a true thyrse. A similar reduction series occurs in *Tambourissa,* ultimately resulting in a monochasium.

In *Monimia ovalifolia,* the ultimate floral units are generally quite contracted, although the secondary axes may be elongated, with up to 87 flowers per inflorescence. The inflorescence of *M. amplexicaulis* is invariably short and contracted, consisting of not more than 37 flowers in specimens I have examined. Inflorescence structure is much more variable in *M. rotundifolia,* ranging from short and contracted to lax and elongated with up to 76 flowers. Plants of the latter type were described as *M. citrina* by Tulasne. Such variation may occur within a single population, e.g., at Col de Bellevue, Réunion (*Lorence 2471–2474*; *2773–2775,* all MO). In view of the variability of inflorescence structure in *Monimia,* it is not a particularly useful taxonomic character.

The basic inflorescence unit in the three species of *Decarydendron* (all monoecious) is a sexually mixed or unisexual pleiochasium (termed "spiciform" by Danguy, 1928). It consists of an elongated floral axis bearing two to four decussate or subalternate pairs of pedicellate androecious

TABLE 5. Selected gross morphological features of *Tambourissa* species according to Group.

Species	Group	Distr.	Vegetat. Pubesc.	Phyllotaxis	Leaf Marg.	Inflr. Posn.	Inflr. Type	Inflr. Composn.
T. thouvenotii	1A	Mad.	velutin.	opposite	toothed	rami., axil.	pleiochasium, solit.	mixed
T. trichophylla	1A	Mad.	pilose-tomentose	opposite	toothed	rami., axil.	pleiochasium	mixed
T. uapacifolia	1A	Mad.	velutin.	opposite	entire	rami.	pleiochasium	unisex.
T. decaryana	1B	Mad.	pilose-hirsute	opposite	entire	cauli.	pleiochasium	unisex.
T. hildebrandtii	1B	Mad.	villous	opposite	entire	rami., axil.	pleiochasium, solit.	mixed
T. humbertii	1B	Mad.	hirsute	opposite	entire	cauli.	fascic., pleiochasium	unisex.
T. nitida	1B	Mad.	pilose	opposite	entire	axil.	pleiochasium, solit.	mixed
T. nosybensis	1B	Mad.	pilose	opposite	entire	cauli.	pleiochasium	unisex.
T. floricostata	1C	Mad.	subglab.	opposite	entire	rami., axil.	pleiochasium, solit.	unisex.
T. parvifolia	1C	Mad.	subglab.	opposite	entire	rami.	pleiochasium	unisex.
T. beanjadensis	2A	Mad.	glabrous	opposite	entire	rami.	pleiochasium	unisex.
T. comorensis	2A	Gde. Comore	subglab.	opposite	entire	rami., cauli.	pleiochasium	mixed
T. crassa	2A	Réun.	subglab.	opposite	entire	term.	solit.	unisex.
T. elliptica	2A	Réun.	subglab.	opposite	entire	cauli., rami., axil.	fascic., pleiochasium, solit.	mixed (unisex.)
T. leptophylla	2A	May.	finely pubesc.	opposite	entire	cauli., rami., axil.	thryse, pleiochasium, solit.	unisex. (mixed)
T. madagascariensis	2A	Mad.	subglab.	opposite	entire	rami.	pleiochasium	unisex.
T. kirkii	2B	Anj.	hirsute	opposite	entire	?	pleiochasium	unisex. (?)
T. paradoxa	2B	Anj.	glabrous	opposite	entire	rami., axil.	pleiochasium, solit.	unisex.
T. capuronii	3	Mad.	glabrous	opposite	entire	cauli.	pleiochasium	unisex. (mixed)
T. moheliensis	3	Moh.	subglab.	opposite	entire	cauli., rami.	thyrse, pleiochasium	unisex.
T. gracilis	4	Mad.	glabrous	opposite	entire	rami.	pleiochasium	unisex.
T. purpurea	4	Mad.	glabrous	opposite	entire	rami., axil., term.	pleiochasium, dichas., solit.	mixed, unisex.

TABLE 5. Continued.

Species	Group	Distr.	Vegetat. Pubesc.	Phyllotaxis	Leaf Marg.	Inflr. Posn.	Inflr. Type	Inflr. Composn.
T. religiosa	4	Mad.	glabrous	opposite	entire	rami., axil., term.	pleiochasium, dichas., solit.	mixed, unisex.
T. amplifolia	5	Maur.	subglab.	opposite	entire	cauli. (rami.)	pleiochasium, fascic, solit.	mixed, unisex.
T. cocottensis	5	Maur.	glabrous	opposite	entire	cauli.	fascic., solit.	unisex.
T. cordifolia	5	Maur.	glabrous	opposite	entire	rami., cauli.	solit., fascic.	unisex.
T. pedicellata	5	Maur.	subglab.	opposite	entire	rami., cauli.	pleiochasium, dichas.	unisex. (mixed)
T. tau	5	Maur.	subglab.	opposite (in pseudoverticels)	entire	cauli., rami., axil.	dichas., fascic., solit.	unisex., mixed
T. tetragona	5	Maur.	glabrous	opposite	entire	cauli.	pleiochasium	unisex.
T. bathiei	6	Mad.	hirsute	opposite	entire	cauli.	pleiochasium, thyrse	unisex.
T. sieberi	6	Maur.	velutin.-toment.	opposite	entire	cauli.	thyrse, pleiochasium	unisex.
T. perrieri	7	Mad.	subglab.	opposite	entire	cauli.	pleiochasium	unisex., mixed
T. quadrifida	7	Maur.	glabrous	opposite	entire	cauli. (rami.)	thyrse, pleiochasium	unisex. (mixed)
T. alaticarpa	8	Mad.	villous	opposite	toothed	cauli.	pleiochasium	mixed (unisex.)
T. longicarpa	8	Mad.	velutin.	opposite	toothed	cauli.	pleiochasium	mixed (unisex.)
T. castri-delphinii	9	Mad.	glabrous	ternate	entire	rami.	pleiochasium, fascic.	unisex.
T. ficus	9	Maur.	pilose-tomentose	ternate	entire	cauli.	solit., fascic.	unisex. (mixed)
T. peltata	9	Maur.	glabrous	ternate	entire	rami. (cauli.)	solit., fascic.	unisex.

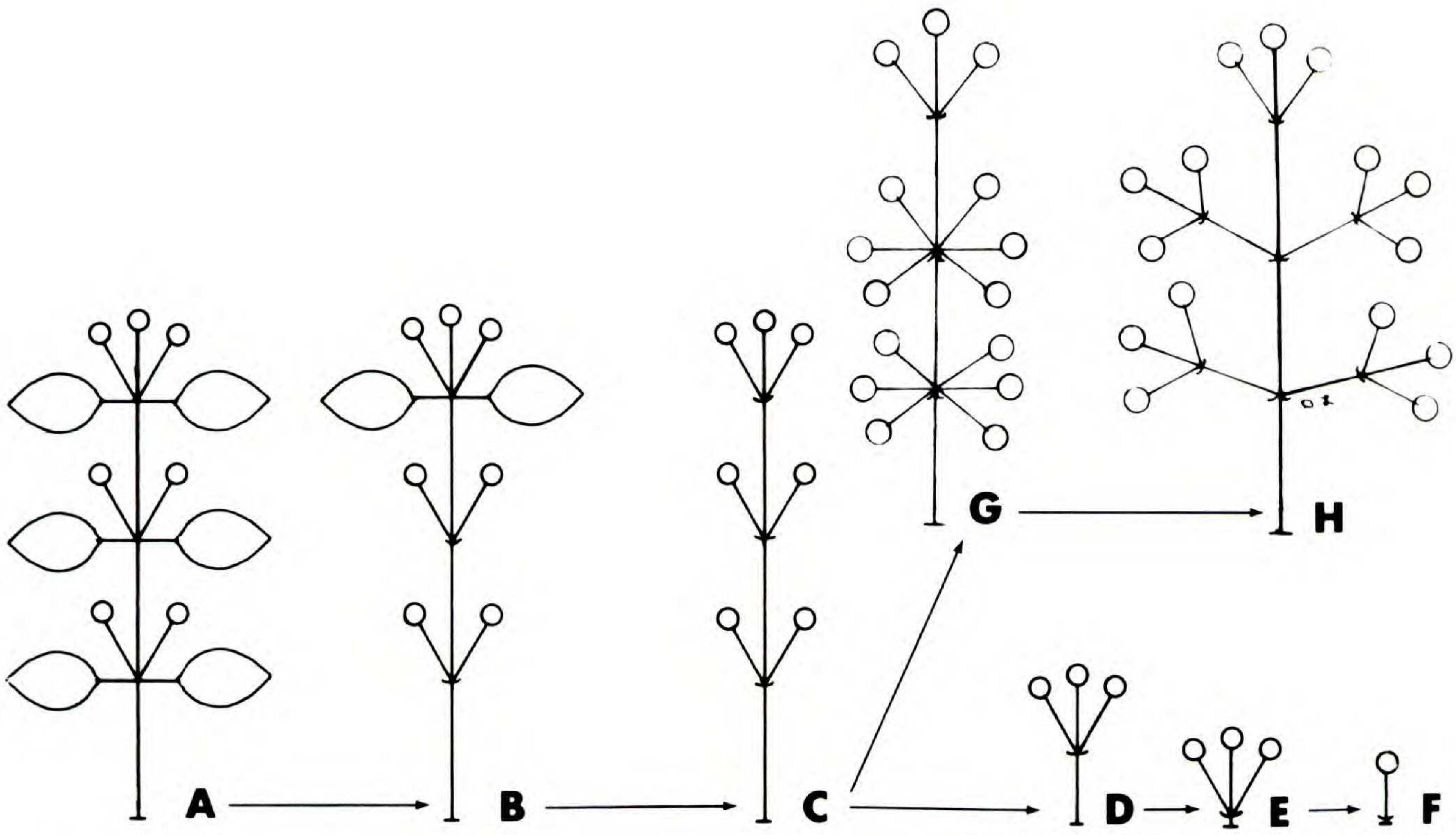


FIGURE 11. Schematic diagrams of *Tambourissa* inflorescence types showing hypothetical reduction (A–F) and elaboration (C, G, H) series.—A, B. Leafy pleiochasia.—C. Pleiochasium.—D, E. Dichasia.—F. Monochasium.—G. Pleiochasium.—H. Thyrse. Flowers are depicted as being in one plane, whereas they are actually decussately arranged. Not to scale.

flowers terminated by a single gynoecious or androecious flower. In all three species the floral axis and pedicels are velutinous or puberulent and the pedicels are generally minutely bracteolate (Fig. 14E). The inflorescence is usually basally cauliflorous in *D. perrieri,* and cauli- or ramiflorous in *D. lamii* and probably also in *D. helenae.*

In *Ephippiandra* (all monoecious), the inflorescence is a sparsely to densely pubescent dichasium or fascicle, or the flowers may be solitary. In *E. capuronii, E. domatiata, E. madagascariensis,* and *E. tsaratanensis* it is an axillary three- or five-flowered sexually mixed dichasium produced on the new growth (Fig. 14F, G). The terminal, central gynoecious flower appears to mature first in the dichasium, after which the lateral androecious flowers come into anthesis. In *E. myrtoidea,* the androecious flowers are axillary, either solitary or in three-flowered fascicles or dichasia, whereas the gynoecious flower is terminal, either solitary or in a three- or five-flowered dichasium with lateral androecious flowers. A similar pattern occurs in *E. microphylla,* although the flowers are solitary with the androecious flowers being axillary and the gynoecious flowers terminal on the stems. In all the species, the short to long floral pedicels are subtended by a pair of acute bracteoles and the peduncles may also be bracteolate.

Tambourissa displays a diverse array of inflorescence types, ranging from elaborate multiflowered thyrses on the one hand to extremely reduced, single-flowered monochasia on the other (Table 5). Pubescence of the floral axes and pedicels varies greatly, from totally glabrous to densely velutinous-tomentose. In all species the pedicel is subtended by one or rarely several minute bracteoles, and the floral axis also bears several pairs of decussate bracteoles basally. Pedicel length is relatively constant for a given species.

A short, determinate pleiochasium is the most widespread inflorescence type in the genus, occurring occasionally or consistently in 32 of the 43 species. This inflorescence type consists of a number of decussately arranged floral pairs spaced along a short to elongated floral axis (Fig. 11C). Although pleiochasia of this type are unisexual in many species (e.g., *T. tetragona*), in others the flowers may be randomly mixed sexually (e.g., *T. pedicellata*), and in yet others they are frequently terminated by a single gynoecious flower with lateral androecious flowers (e.g., *T. hildebrandtii, T. longicarpa*). In this case the flowers of one sex (usually gynoecious) generally open first and it is therefore a cyme in the classical sense (e.g., Lawrence, 1951). The pleiochasia may be axillary, ramiflorous, or rarely cauliflorous.

The pleiochasial inflorescence may be derived from a leafy stem with solitary, axillary, and terminal flowers by gradual reduction of the leaves into bracteoles, and by a concomitant shortening of the main axis (Fig. 11A–C) similar to that described for *Monimia.* Single individuals of species such as *T. elliptica* (*Lorence 2528,* MO) and *T. pedicellata* (*Lorence 2584–2586,* all MO) often show the entire range of stages in the reduction series. As *Tambourissa pedicellata* is one of the least specialized species in terms of floral morphology, it may have possibly retained an unspecialized inflorescence type as well. Gottsberger (1974) considers lateral flowers or few-flowered inflorescences to be unspecialized in primitive angiosperms, from which other types have been derived.

Further shortening and reduction of the pleiochasium ultimately results in a dichasium of three flowers supported by a short peduncle (Fig. 11D, E), which may either be ramiflorous as in *Tambourissa castri-delphinii,* a dioecious species, or terminal and axillary as in *T. purpurea* and *T. religiosa,* which have sexually mixed dichasia or pleiochasia. Suppression of both lateral flowers thus results in a single-flowered monochasium (Fig. 11F), as in *T. ficus* or *T. tau,* which are cauli- and ramiflorous respectively, and in *T. crassa,* which has terminal flowers. Many of the cauliflorous species are subdioecious or dioecious and produce clusters or fascicles of monochasia from knobby meristematic swellings on the trunk. That the pedicel is jointed to a distinct peduncle, where it often bears one of more pairs of decussate bracteoles, suggests that it is a reduced inflorescence and not merely a solitary flower per se. Ontogenetic studies are required to confirm this, however.

At the opposite extreme, a number of species have compound inflorescences with numerous flowers that may be derived by an elaboration of the pleiochasium. In species such as *Tambourissa quadrifida* (Group 7), there has been a multiplication of the floral pairs into cymose or umbelloid units of three to five flowers (Figs. 11G, 20B).

The two species in Group 8 (*T. alaticarpa* and *T. longicarpa*) also possess pleiochasia with the androecious flowers produced in lateral umbelloid or cymose groups of one to three, whereas one to three gynoecious flowers are segregated in a terminal unit (Fig. 17A). The terms cymose and umbelloid are used loosely here, as the flowers of a group may either mature simultaneously or in a staggered, random fashion. Pleiochasia with terminal gynoecious and lateral androecious flowers also occur in *T. perrieri* (Group 7) and *T. hildebrandtii* (Group 1B).

Floral units in other species such as *T. sieberi* and *T. bathiei* (Group 6) are produced on distinct peduncles and the resulting inflorescence is thyrsic (Fig. 11H). In these species, the inflorescences tend to be cauliflorous and predominantly unisexual, although flowers of the opposite sex are occasionally intermixed.

In summary, although inflorescence type and position may vary considerably in the four genera discussed above, they are frequently modally distinct for given species and often provide a number of taxonomically important features.

FLORAL MORPHOLOGY AND ANATOMY

In terms of floral morphology, the Monimiaceae are an extremely diverse, and at the same time, coherent family in which many of the genera exhibit trends towards floral specialization, often via reduction (Perkins & Gilg, 1901; Perkins, 1911, 1925; Money et al., 1950). The following general evolutionary trends in the Monimiaceae sensu lato have been summarized by Corner (1976) and Endress (1980b):

1) Transition from floral bisexuality to unisexuality.
2) Reduction in size and number of parts.
3) Transition from spiral, to radial, to decussate arrangement of parts.
4) Massive development of the receptacle (floral cup) which assumes the functions of a perianth and ovary wall.
5) Closure of the receptacle, involving:
    A) Enclosure of the inner tepals by the receptacle.
    B) Enclosure of the carpels (ovaries) by the female receptacle.
    C) Permanent closure of the gynoecious receptacle, which dehisces only in fruit.
    D) Enclosure of the stamens by the androecious receptacle, which splits open flat by lateral fissures at anthesis, or remains partly closed.
6) Transition from free, stalked, or sessile carpels borne on the flattened or shallow receptacle, to inferior syncarpous carpels immersed in the receptacle wall.

7) Production of a mucilaginous compitum, and finally a "hyperstigma" which assumes a stylar function.
8) Apical (or rarely basal) fusion of the anther loculi into a single loculus with a progressive shortening and broadening of the filament.

Although many of these trends are most apparent at the subfamilial or tribal levels (see discussion under Taxonomic History of the Monimiaceae), a significant number also occur within the Mollinedioideae (sensu Thorne) and occasionally within a single genus (e.g., *Tambourissa*). The four genera belonging to the two subfamilies discussed here are all relatively specialized, i.e., have unisexual flowers lacking an elaborate petaloid perianth. Although *Monimia* displays a number of the same features as the other three genera, it will be discussed first as it belongs to a separate subfamily, the Monimioideae. Because the other three genera, all Mollinedioideae, display obvious trends involving three levels of specialization and form a natural coherent series, they will be discussed as such.

Floral construction in *Monimia* is reduced, highly specialized, and very similar in all three species. Flowers of both sexes have closed, globular receptacles in bud surmounted by three to six minute, decussate, scale-like tepals (Perkins & Gilg, 1901; Money et al., 1950). In *Monimia*, the receptacle has assumed the function of the perianth and in the gynoecious flowers turns orange or red at anthesis. The globose, internally pubescent gynoecious receptacle encloses several free, subsessile carpels, each with a single pendulous, anatropous ovule. At anthesis, the receptacle opens by means of a small, three to six lobed apical pore through which the glistening, slightly papillose white styles are exserted (Figs. 12.1A, 14B).

At anthesis, the androecious flower splits open by lateral fissures into four to six valvate, ultimately recurved lobes with numerous (ca. 25–150) irregularly disposed, white bisporangiate stamens. Each stamen bears a pair of white, ear-like appendages at or near its base (Fig. 12.1C, D). Anther dehiscence is lateral along the inner, adaxial margins of the monosporangiate loculi, which then open outward like flaps (Figs. 12.1D, 13A) releasing the slightly coalescent pollen. Staminal dehiscence in *Monimia* has been described as subintrorse by Hutchinson (1964), but is more nearly introrse (De Candolle, 1868; Perkins & Gilg, 1901). Observations on living flowers of all three species revealed no apparent nectar production by the stamens as in some Atherospermoideae (Sampson, 1969a), although sweet odors are emitted by flowers of both sexes.

Obvious floral morphological differences in the species are expressed in terms of receptacle size (smallest in *Monimia ovalifolia*), number of stamens (fewest in *M. ovalifolia*, most numerous in *M. amplexicaulis*), and in stamen length (shortest in *M. ovalifolia*, longest in *M. rotundifolia*). Flowers of both sexes are externally pubescent, and trichomes furnish additional useful specific characters. A more detailed study of the ontogeny and floral construction in *Monimia* is forthcoming (Endress & Lorence, in prep.).

The three genera belonging to the Mollinedioideae form a natural series in which three evolutionary levels of floral morphological specialization are obvious, primarily in the gynoecious flowers. The least specialized genus is *Decarydendron*, and the most specialized is *Tambourissa* (Fig. 12.2–12.4).

1) *Decarydendron:* receptacles of both sexes are shallowly cupuliform and open gradually without splitting at anthesis; tepals are large, numerous, in radial series; carpels are free, numerous, long and clavate, subsessile; fruiting carpels are presumably exposed (?); stamens have a distinct filament and separate loculi (Fig. 12.2A–D).

2) *Ephippiandra* (including *Hedycaryopsis*): gynoecious receptacles are discoid and develop gradually without splitting at anthesis; tepals are few, small, decussate; carpels are free, fewer and shorter, columnar, sessile; fruiting carpels are basally immersed in the receptacle; androecious receptacle is closed in bud, splitting open by longitudinal fissures at anthesis; stamens are subsessile, with short, broad filaments, loculi are free or confluent (Fig. 12.3A–D).

3) *Tambourissa* (including *Phanerogonocarpus*): gynoecious receptacle is closed, globular to cylindrical, the apex often splitting partly open at anthesis; tepals are few, minute, decussate; carpels are inferior, syncarpous; fruiting carpels are enclosed; fruiting receptacle splits open at maturity; androecious receptacle is closed in bud, splitting open by longitudinal fissures at anthesis; stamens have distinct filaments or are short and sessile, loculi are free or confluent (Fig. 12.4A–D).

Both androecious and gynoecious flowers of *Decarydendron* are relatively monomorphic, somewhat subglobose in bud, and have seven to 15 large, thick, obtuse tepals in two or three

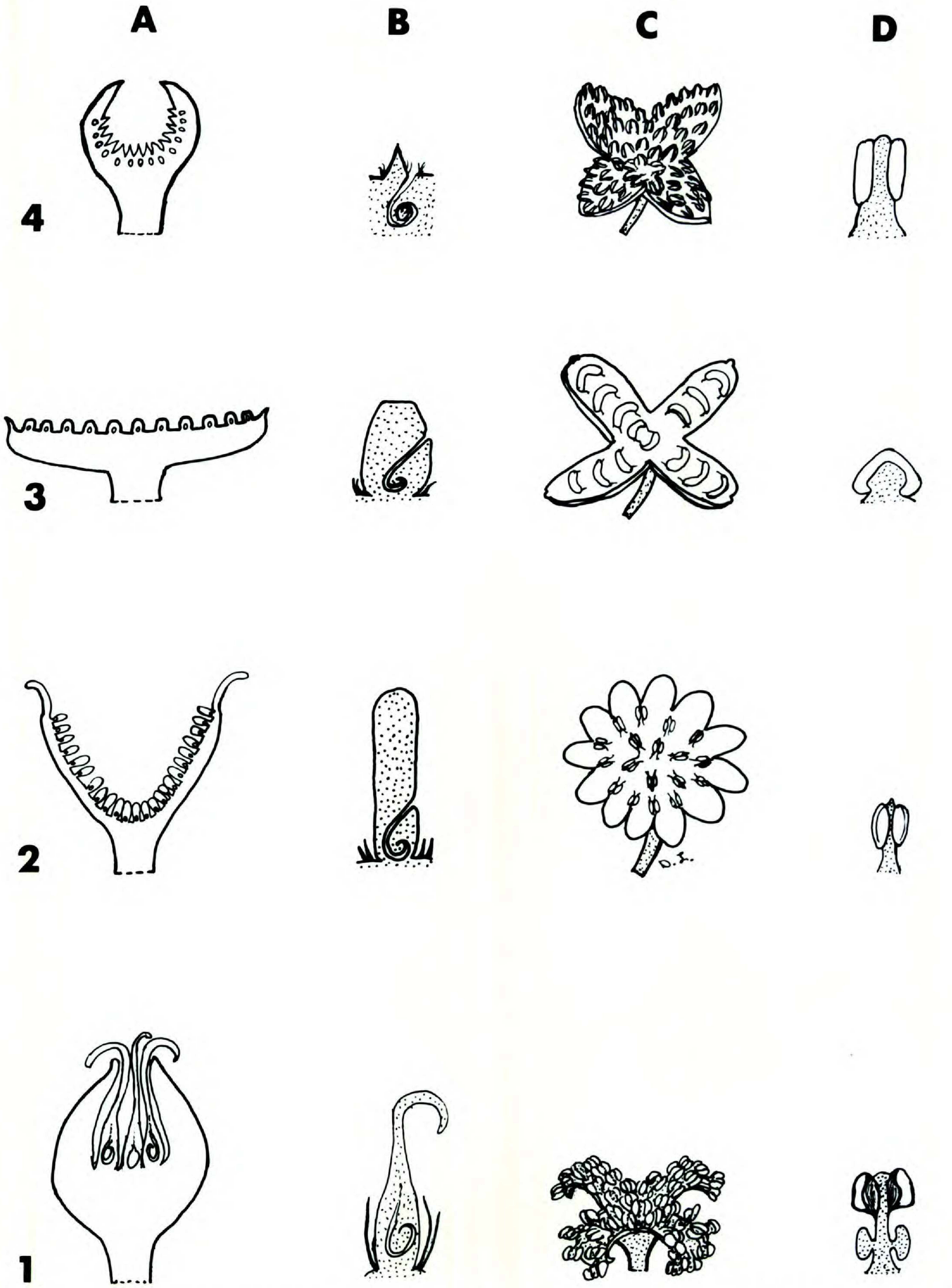
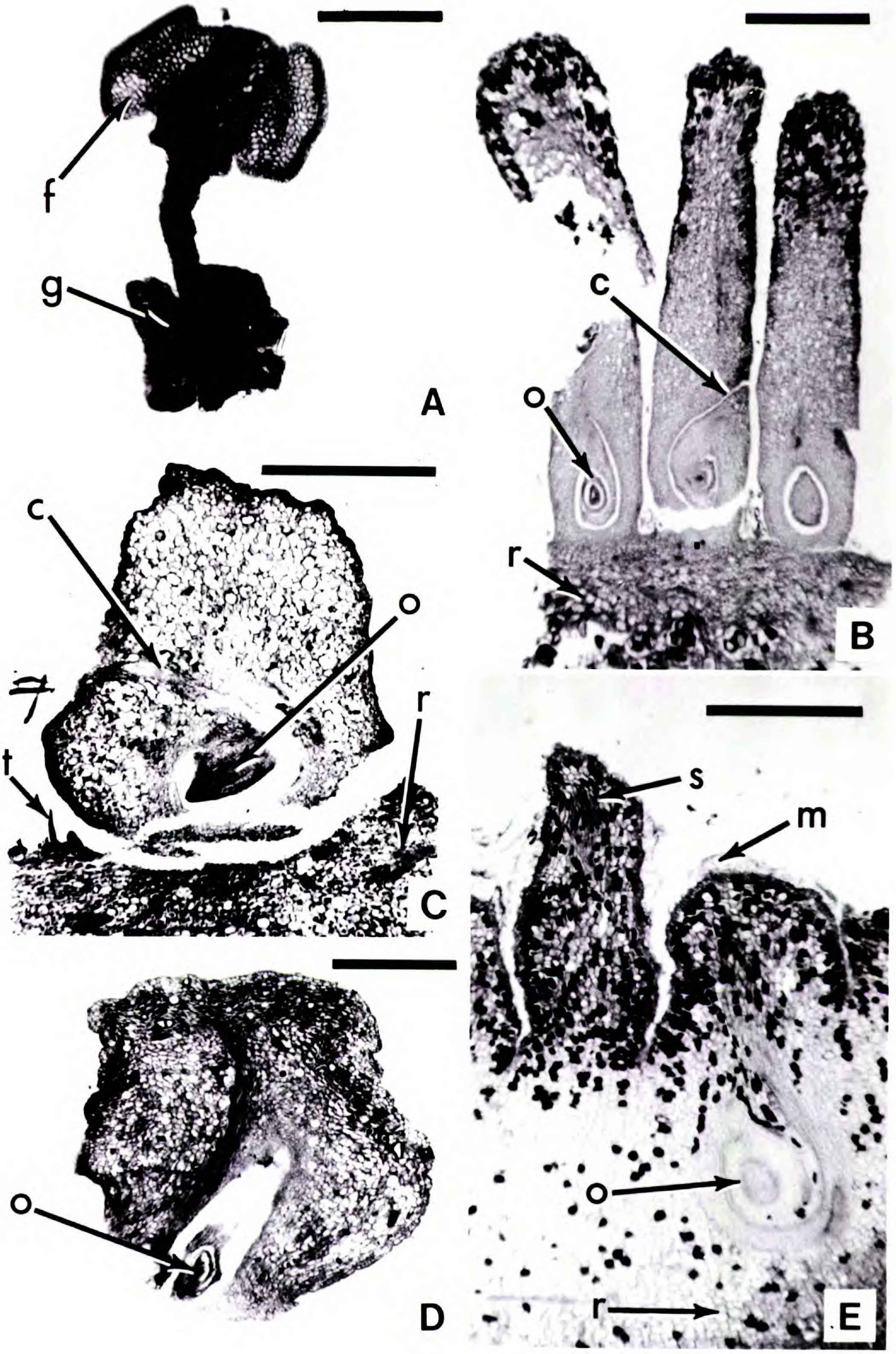


FIGURE 12. Schematic drawings of flowers of the four genera of Monimiaceae in the Malagasy region. 1. *Monimia*; 2. *Decarydendron*; 3. *Ephippiandra*; 4. *Tambourissa*.—A. Gynoecious flower, longitudinal section.—B. Individual carpel, longitudinal section.—C. Androecious flower at anthesis.—D. Stamen. Not to scale.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whorled series. The tepals are infolded in bud and the flowers consequently do not split, but open gradually at anthesis as the tepals become erect or everted. The external receptacle surface is often pubescent with simple trichomes.

At anthesis the gynoecious flower of *Decarydendron* is hemispherical or obconical with thick walls and straight or slightly incurved tepals. Numerous free, clavate carpels line the inner receptacle surface (ca. 300 in *D. helenae*) and are interspersed with short, densely tufted simple lignified trichomes. In *D. helenae* var. *stenophyllum* (*Humbert 6613,* K), each carpel is clavate or cylindrical, ca. 1.5 mm long, slightly constricted basally and obtuse apically (Fig. 13B). A single, pendulous anatropous bitegmic ovule is contained in a small loculus which is confined to the base of the carpel and from which the oblique stylar canal runs upward and opens at the side of the carpel in its basal third (Fig. 13B). The carpellary ground tissue contains scattered oil cells above the ovary and densely aggregated stone cells in the terminal portion (Fig. 13B). Stone cells also occur in the receptacular ground tissue, but no tanniferous idioblasts were observed. In cleared carpels, a single vascular bundle enters from the base, supplies the ovule, and extends upward almost to the apex, terminating in tracheoids. The exterior surface of the carpel is possibly secretory in nature as in many Monimiaceae (Endress, 1980b), but no traces of mucilage were observed.

In the androecious flower, from 16 to 60 stamens are irregularly dispersed over the glabrous to pubescent inner surface of the shallowly concave or cupuliform receptacle (Figs. 12.2C, 14E). Stamens of all three species are comparatively unspecialized with a distinct, narrow filament, unprolonged connective, and separate, laterally dehiscent, tetrasporangiate anthers (Fig. 12.2D).

Useful taxonomic features of *Decarydendron* flowers include: number and size of tepals and characters of their margins (crenulate or not); number of stamens; size of the receptacle and presence or absence of lateral ridges (Cavaco, 1959). The genus is clearly the least specialized florally of the Mollinedioideae in the Malagasy region.

Floral construction in *Ephippiandra* (including *Hedycaryopsis*) is more specialized, including a strong male/female floral dimorphism (Figs. 12.3A–D, 14F, G). Gynoecious flowers are somewhat globular and concave in bud, but open gradually and become discoid during ontogenetic development. In *Ephippiandra madagascariensis* (*Bernardi 11977,* K, MO), the receptacular rim initially bears four small, decussate, deltoid tepals which apparently divide once by lateral doubling, resulting in eight tepals in the mature flower. Most species also appear to have four, eight, or rarely 16 minute, decussate tepals, and the receptacles are externally pubescent with short to long simple hairs. At anthesis the receptacle is flat and discoid, crowded with 20–150 free, sessile, shortly columnar carpels interspersed with clusters of simple, lignified trichomes (Fig. 12.3A, B). Each carpel is four to six sided, ca. 1–1.5 mm long, with a flat top, straight to inclined sides, and a slightly constricted base (Fig. 13C, D). The solitary ovule is anatropous or amphitropous and bitegmic, situated in a small loculus near the base of the carpel, with a stylar canal leading obliquely upward and opening at the side near the middle of the carpel (Fig. 13C, D). The entire carpel is covered by an epidermal layer which appears to be secretory and produce mucilage at least around a central zone. Occasional short, simple hairs occur on the carpellary surface in *E. madagascariensis.* In cleared carpels, two vascular bundles enter from the base on either side of the ovule in *E. myrtoidea, E. madagascariensis,* and *E. tsaratanensis,* and fan out into a zone with numerous, terminal tracheoids near the apex. Endress (1980a) also found tracheoids in other genera and suggested that they might function as water storage cells. The ventral bundle gives rise to a weak, arcuate secondary branch supplying the ovule. The floral ground tissue of *E. myrtoidea* contains oil cells, stone cells, and large numbers of tanniferous idioblasts. That of *E.*

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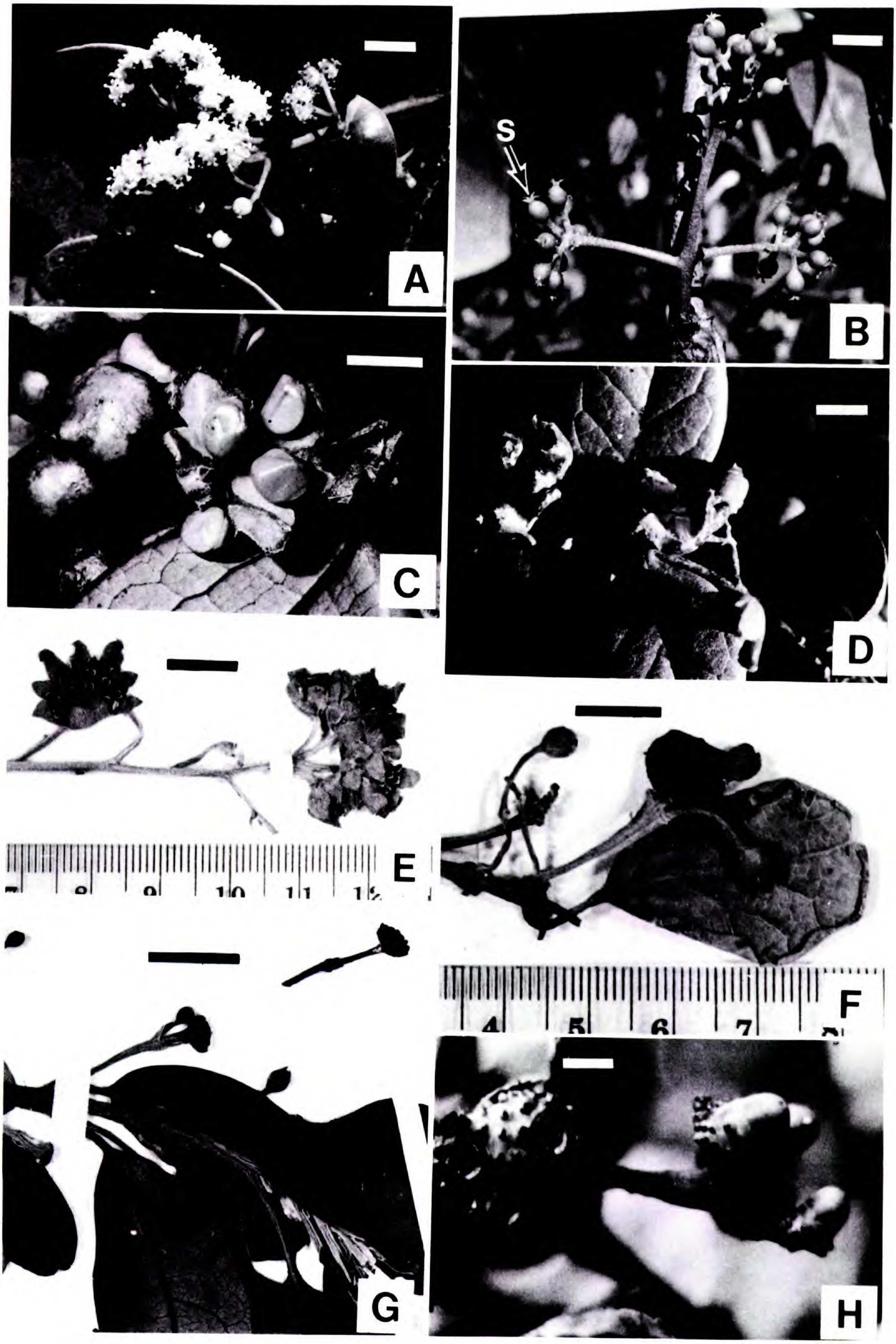
FIGURE 13. Photomicrographs of floral parts.—A. Stamen of *Monimia amplexicaulis* showing nearly introrse dehiscence and basal glands, whole mount, *Lorence 2444* (MO).—B. Carpels of *Decarydendron helenae* var. *stenophyllum,* longitudinal section, *Humbert 6613* (K).—C. Carpel of *Ephippiandra madagascariensis,* longitudinal section, *Bernardi 11977* (MO).—D. Carpel of *E. myrtoidea,* longitudinal section, *Parker s.n.* (K).—E. Carpel of *Tambourissa cordifolia,* longitudinal section, *Lorence 2630* (MO). Bars equal 0.5 mm. c = canal leading to ovule; f = flap of anther loculus; g = glands at base of stamen; m = mucilaginous exudate; o = ovule; r = receptacular ground tissue; s = style; t = trichome.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tsaratanensis contains both oil cells and numerous tanniferous cells, whereas only oil cells occur in *E. madagascariensis.* Receptacular ground tissue of these three species contains idioblasts comparable to those found in the carpels. The fewer and shorter, sessile carpels and reduced, decussate tepals of *Ephippiandra* represent specializations in comparison with *Decarydendron.*

Androecious flowers of *Ephippiandra* are globular and closed in bud (Fig. 14F, G), externally pubescent with short to long simple hairs, and generally bear four pairs of small to minute, acute to deltoid, decussate tepals at or near the apex (Fig. 12.3C, D). At anthesis, the floral cup splits by lateral fissures into four subequal, valvate segments exposing the 9–50 stamens (Fig. 12.3C, D) scattered or situated in several series on the glabrous to pubescent inner receptacle surface. The apex of each lobe usually bears one or rarely two obtuse, scale-like tepals in all but *E. myrtoidea.* The tetrasporangiate stamens range from ligulate and incurved to short, broad, and obtusely deltoid. Those of *E. domatiata, E. madagascariensis, E. perrieri,* and *E. tsaratanensis* are somewhat longer with more distinct filaments, separate loculi, and slightly prolonged or apiculate connectives, whereas those of *E. microphylla* and *E. myrtoidea* are generally shorter and sessile or subsessile with the loculi apically connivent or confluent into a single, crescentiform loculus. Staminal types within the genus intergrade, however, and a comparable range of variation occurs in *Tambourissa.* Dehiscence is lateral and longitudinal, but is continuous in stamens with a single, crescentiform loculus (both separate and confluent loculi may occur in a single flower, e.g., *E. myrtoidea*). *Ephippiandra microphylla* and *E. myrtoidea* have few (10–18), highly reduced stamens with connivent or confluent loculi; these represent specialized features.

Taxonomically useful characters in *Ephippiandra* flowers include: size of the receptacle; number of carpels, stamens, or tepals; presence or absence of tepals on the inner receptacle lobes; size and shape of tepals; size and shape of stamens; condition of the loculi (free or confluent). Floral reduction in the genus shows specialization over *Decarydendron.*

Floral construction in *Tambourissa* (including *Phanerogonocarpus*) displays a number of still more specialized trends, one being a strong androecious/gynoecious floral dimorphism (Fig. 12.4A–D), except in *T. pedicellata, T. purpurea,* and a few other species. Perhaps the most striking and important trend is apparent in the gynoecious flowers, which have their carpels immersed in and fused with the receptacular wall and are therefore inferior and syncarpous (Endress, 1979, 1980b), thus showing considerable advancement over *Decarydendron* and *Ephippiandra.* Although androecious flowers of some *Tambourissa* species are comparable to those of *Ephippiandra,* those of other species are even more specialized. Because a more detailed study of the ontogeny and floral construction of *Tambourissa* has been published elsewhere (Endress & Lorence, 1983), only a brief account is given here.

Gynoecious flowers of *Tambourissa* consist of a massively developed receptacle which is generally closed in bud. Considerable variation occurs in receptacle size and morphology, the main types of which are shown in Figure 15. The receptacle is more or less napiform or cup-like in the majority of species (e.g., *T. cordifolia, T. ficus, T. pedicellata*; Fig. 15B, C, J), but ranges from flat and discoid in *T. peltata* (Fig. 15A), to closed and spherical in *T. sieberi,* or even cylindrical in *T. alaticarpa* and *T. longicarpa* (Fig. 15E, H). Both the flat, open and the closed, globose or cylindrical types appear to be highly specialized and derived from a more generalized cupuliform type like that found in *T. pedicellata.* The receptacles of *T. alaticarpa* and *T. longicarpa,* although extremely elongated and laterally winged, still fall within the range of variation displayed by certain other species. For example,

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FIGURE 14. Flowers and fruits.—A. *Monimia ovalifolia,* androecious inflorescence at anthesis, *Lorence 2896* (MO).—B. *M. ovalifolia,* gynoecious inflorescence at anthesis, note exserted styles (s), *Lorence 2757* (MO).—C. *M. ovalifolia,* ripe fruiting receptacles splitting to expose carpels, *Coode 4954* (K).—D. As for C, *Lorence 2350* (MO).—E. *Decarydendron lamii,* terminal portion of androecious inflorescence with expanded androecious flower showing stamens and large tepals, *Lam & Meeuse 5835* (P).—F. *Ephippiandra madagascariensis,* inflorescences showing globose androecious flowers in bud and central discoid gynoecious flower, *Ursch 66* (P).—G. *E. perrieri,* flowering stem showing globose androecious flowers in bud and discoid central gynoecious flower, *Perrier de la Bâthie 16249* (P).—H. *E. tsaratanensis,* old infructescence with carpels gone (left), and submature infructescence with three green carpels seated in basal cupules (right), *Gentry 11605* (MO). Bars equal 10 mm.

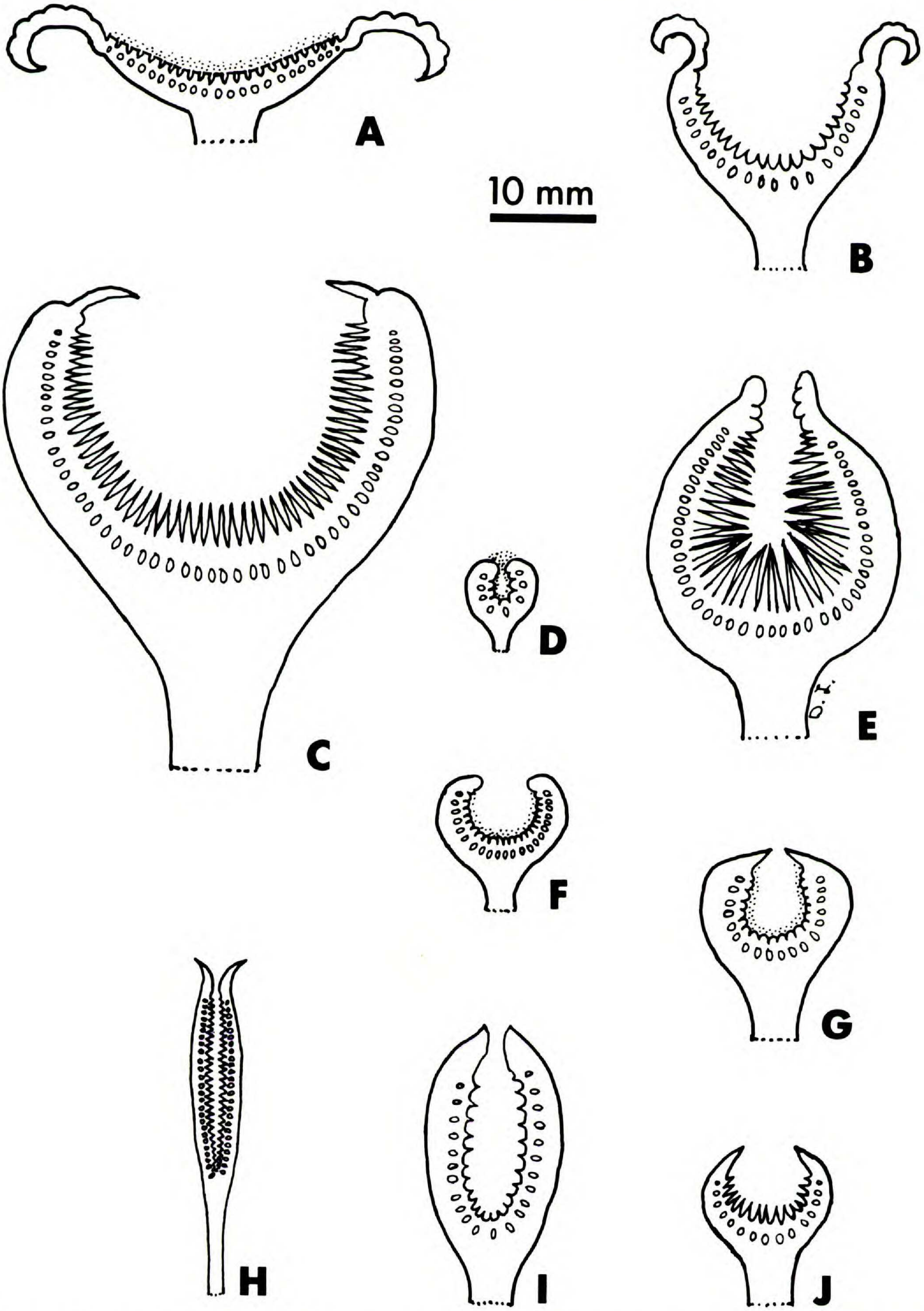


FIGURE 15. Schematic longitudinal sections through gynoecious floral receptacles of some *Tambourissa* species.—A. *T. peltata*.—B. *T. cordifolia*.—C. *T. ficus*.—D. *T. purpurea*.—E. *T. sieberi*.—F. *T. comorensis*.—G. *T. elliptica*.—H. *T. alaticarpa*.—I. *T. quadrifida*.—J. *T. pedicellata*. Stippled areas represent mucilaginous compitum. Drawn to approximate scale.

gynoecious receptacles of *T. quadrifida* are cylindrical-ellipsoid, and those of *T. floricostata* bear four lateral, longitudinal ridges. The external receptacular surface in the genus ranges from glabrous (e.g., *T. tetragona*) to densely velutinous (e.g., *T. sieberi*) or corky (e.g., *T. tau*).

The gynoecious bud apex in *Tambourissa* generally bears several pairs of minute, decussate obtuse or deltoid, scale-like tepals. Two pairs are usually visible externally in most species, and these are sometimes fused into an apicule (e.g., in *T. sieberi, T. tau*). In *T. purpurea* there are usually five pairs; the innermost are enclosed in the floral cup and intergrade into the carpels (Endress, 1980b; as *T. religiosa*). In several of the Comorean species in Group 2 (*T. comorensis,* Figs. 15F, 17B; *T. kirkii*; and *T. leptophylla*) where the gynoecious receptacle remains open during the entire floral development, the tepals are apparent only during the very young stages. This is an unusual feature within the genus, and could represent either a highly advanced character or, alternatively, a transitional stage between the open, discoid receptacles of *Ephippiandra* and the closed buds of most *Tambourissa* species. At floral anthesis, the receptacles of most species generally split open by shallow (e.g., *T. purpurea*) to deep (e.g., *T. peltata*) longitudinal fissures between the tepals, forming a number of subequal lobes ranging from four in most species (e.g., *T. cordifolia,* Fig. 42G, H) to as many as eight or ten in *T. ficus* (Fig. 15C) and *T. tau* (Fig. 39E). The sterile internal surface of the lobes may be pubescent (e.g., *T. moheliensis,* Fig. 36E) or glabrous (*T. tau*). Inner lobes of *T. peltata,* and to a lesser degree *T. cordifolia,* are sculptured with longitudinal ridges or lines, somewhat verrucose in the former species and bearing stomata in both species (Endress & Lorence, 1983). Position of the lobes at anthesis ranges from incurved (e.g., *T. pedicellata,* Fig. 15J), or erect (e.g., *T. hildebrandtii*), to spreading-reflexed (e.g., *T. peltata*; Figs. 15A, 17E). The colorful, everted lobes of *T. peltata* have assumed the function of the perianth.

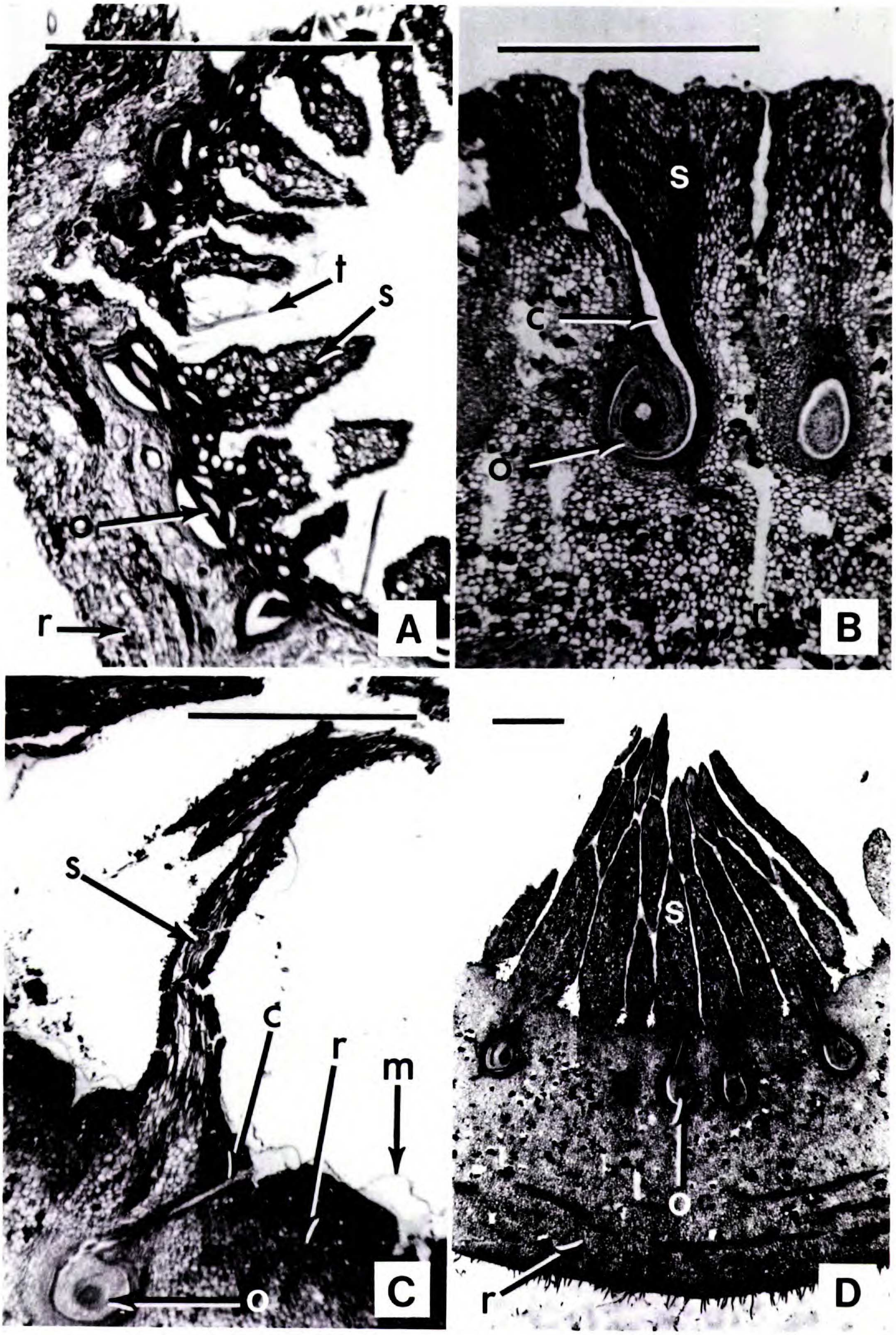
The carpels of *Tambourissa* are immersed in and united with the receptacle wall and are therefore inferior and syncarpous in a morphological sense (Endress, 1979, 1980b, 1982), not embedded in sockets as stated by Baillon (1871) and Corner (1976). Each carpel is unilocular with a solitary, bitegmic, anatropous ovule (amphitropous in *T. decaryana, T. nosybensis*). The two species formerly included in *Phanerogonocarpus* (*T. alaticarpa* and *T. longicarpa*) also possess this type of carpel (Fig. 16A). The inner receptacle surface may be glabrous (e.g., *T. tau*; Fig. 16C) or interspersed with dense tufts of short, simple lignified trichomes (e.g., *T. sieberi*; Fig. 16D).

The number of carpels varies greatly between species, is proportional to the size of the receptacle, and provides a good, species-specific character (Table 6). For example, fresh flowers of *T. purpurea* are only 5–6 mm diam. and have 35–70 carpels, whereas those of *T. ficus* are 35–40 mm diam. and have ca. 1,000–2,000 carpels. Size and shape of the styles are constant and often species-specific features, varying greatly within the genus. Styles of *T. peltata* (Fig. 16B) are short (ca. 0.5 mm long), crowded, and obtusely columnar. Those of *T. tau* (Fig. 16C) are longer (ca. 2–3 mm), free and setose, whereas in *T. sieberi* (Fig. 16D) they are 3–4 mm long, setose and coalescent. A canal was found to run obliquely upward from the ovule before opening at the base of the style in all 31 species examined in this study. This canal has been termed the "ventral slit" by Endress (1980b) and allows passage of the pollen tube for fertilization.

Pollen tube transmission in *Tambourissa* does not occur through the stylar tissue; rather, the site of transmission has shifted to the exterior of the style as in many other genera in the Monimiaceae (Endress, 1979, 1980b). In many species the entire external stylar surface is secretory, producing a mucilaginous exudate through which the pollen tubes grows until encountering the stylar canal and passing through it directly to the ovule. Traces of this mucilage can be seen in Figures 13E and 16C.

A further specialization is a massive mucilage production forming a thick layer lining the floral cup (e.g., *T. peltata*; Figs. 15A, 17E). This "extragynoecial compitum" functionally links and interconnects all the carpels (Endress, 1980b, 1982), enabling pollen grains deposited in one place to cross over and grow to any other carpel, thereby maximizing efficiency of the pollen. It is analogous to the usual intragynoecial compitum (transmitting tissue) in syncarpous gynoecia (Carr & Carr, 1961). The mucilage may also have a nectar function (see chapter on Floral Biology).

In *Tambourissa purpurea,* the extra-carpellary, stigmatic secretory epidermis covers not only the surface of the carpels but also the entire inner orifice of the floral cup including the inner tepals. Termed a "hyperstigma" by Endress (1979,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1980b; as *T. religiosa*), this unique floral construction is the culmination of floral specialization in Monimiaceae. In addition to *T. purpurea* it also occurs in *T. elliptica* and *T. crassa* (Lorence, pers. observ.), as well as *Wilkiea, Kibara,* and *Hennecartia.* (Endress, 1980b). In *T. purpurea,* a mucilaginous plug completely occludes the floral pore and forms a continuous layer extending down to the carpels and functions as the pollen reception and transmission site. In *T. crassa* and *T. elliptica,* the orifice is only occluded early in anthesis, but the mucilage otherwise completely lines the floral cup. A conspicuous mucilaginous exudate was also observed in fresh or rehydrated flowers of *T. decaryana, T. comorensis, T. longicarpa, T. madagascariensis, T. nosybensis, T. peltata,* and *T. beanjadensis* (Table 7).

Each *Tambourissa* carpel is supplied by a single vascular bundle dorsal to the ovule which runs into the style for much of its length. The carpels and receptacular ground tissue of each species characteristically contain varying proportions of one or more types of the following idioblasts: oil cells; tanniferous cells; stone cells. Amount and type of each provide useful, species-specific characters (Table 7).

Androecious flowers of all species of *Tambourissa* are globose to subglobose and closed in bud, usually bearing apically two external pairs of small to minute, free to fused tepals, and one or more additional pairs enclosed in the receptacle. The presence of tepals (as "staminodes") on inner receptacle lobes of the species formerly included in *Phanerogonocarpus* occurs in many species of *Tambourissa* and does not serve to distinguish the two genera as stated by Cavaco (1957c). The external receptacle surface is comparable to that of the gynoecious flower, ranging from glabrous to densely pubescent or corky. Male floral size shows great intraspecific variation, but is often comparable to that of the gynoecious receptacle. Two of the Comorean species, *T. kirkii* and *T. moheliensis* (Figs. 18D, 36D, E) have androecious receptacles that are much smaller than the gynoecious ones, however. The number of stamens is likewise proportional to receptacle size, and is generally somewhat less than the number of carpels in a given species (Table 6). To cite extremes, fresh androecious buds of *T. purpurea* are 5–6 mm diam. with 20–32 stamens, whereas those of *T. ficus* are 45–50 mm diam. and contain ca. 900–1,800 stamens, making it the largest androecious flower in the family!

At anthesis, androecious flowers of most *Tambourissa* species split open by longitudinal fissures between the tepals into generally four or sometimes five (range three to seven) subequal, valvate lobes. The number of lobes and degree to which they split and reflex provide useful, species-specific characters. For example, lobes of *T. pedicellata* (Figs. 17C, 18F) are shallowly fissured, incurved, and scarcely open more than halfway. Those of *T. amplifolia* (Fig. 18B) split about halfway and open flat, whereas those of *T. quadrifida* (Figs. 18I, 19B) split deeply to the base and recurve completely. In some, including *T. purpurea* (Fig. 18E) and Comorean species such as *T. moheliensis* (Fig. 18D), the floral cup merely splits by shallow fissures and remains relatively closed and globose. An extreme form occurs in *T. gracilis* and *T. paradoxa,* which do not split at all; a small pore flanked by tepals provides the only access to the stamens. Such minute, closed flowers and very large, open flowers probably represent highly specialized, extreme forms derived from a more generalized type, perhaps similar to that of *T. pedicellata.*

Stamens of many *Tambourissa* species (e.g., *T. pedicellata*; Fig. 18F) consist of a distinct, broad filament and two lateral, bisporangiate, longitudinally dehiscent, extrorse loculi beyond which the connective is often slightly prolonged. This relatively unspecialized type resembles those found in *Decarydendron* and some species of *Ephippiandra.* Other species of *Tambourissa* display a number of extreme and highly specialized trends. One trend is towards extreme staminal elongation and prolongation of the connective, e.g., in *T. capuronii* (Fig. 18C) with stamens 6–8 mm long. In *T. tau* (Fig. 18H), the loculi occur on extended lateral arms of the connective in the form of a "T." The loculi of *T. ficus* (Fig. 18G) have shifted to an abaxial position with the filament and prolonged connective thickened. In other species such as *T. amplifolia* (Fig. 18B) and *T. peltata* (Figs. 17D, 18A), the loculi are often apically confluent and dehiscence

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FIGURE 16. Styles and carpels of some *Tambourissa* species, longitudinal sections.—A. *T. longicarpa, Capuron 8775-SF* (P).—B. *T. peltata, Lorence 2555* (MO).—C. *T. tau, Lorence 2953* (MO).—D. *T. sieberi, Lorence 2250* (MO). Bars equal 1 mm. c = canal leading to ovule; m = mucilaginous exudate; o = ovule; r = receptacular ground tissue; s = style; t = trichome.

TABLE 6. Selected floral morphological features of *Tambourissa* species according to Group.

Species	Group	Sex	Androecious Flower	Stamens			Gynoecious Flower		Styles	
			Shape at Anth.	No. (ca.)	Connective	Loculi	Shape	Orifice	No. (ca.)	Shape
T. thouvenotii	1A	monoec.	4-fid, flat	50–100	prol.	free	napiform-depressed	4-lobed	100–150	conical
T. trichophylla	1A	monoec.	4-fid, flat	±100	prol.	free	subglobose	4-lobed	100	conical
T. uapacifolia	1A	dioec.?	4-fid, flat	±100	apic.	free	?	?	?	conical
T. decaryana	1B	dioec.?	? ?	?	?	?	napiform-depressed	4–5-lobed	200–300	conical
T. hildebrandtii	1B	monoec.	4-fid, flat	75–90	prol.	free	napiform-subglobose	4-lobed	150–200	conical
T. humbertii	1B	dioec.?	? ?	?	?	?	napiform-depressed	4(–5)-lobed	500	ovoid
T. nitida	1B	monoec.	? ?	60	apic.	free	napiform-turbinate	?	200†	conical
T. nosybensis	1B	monoec.?	4-fid, flat	70	apic.	free	discoid-patelliform	4-lobed	400	conical
T. floricostata	1C	monoec.	4-fid, incurved	16–22	apic.	free	globose-depressed	subcirc.	?	conical
T. parvifolia	1C	monoec.	4-fid, flat	50–60	apic.	free	subglobose-napiform	subcirc.	200†	conical
T. beanjadensis	2A	monoec.	4–5-fid, flat	36	non-prol.	confl.	globose-napiform	4-lobed	200	conical
T. comorensis	2A	monoec.	4-fid, flat	125–150	non-prol.	free	patellif.-urceol.	circul., entire	200†	columnar
T. crassa	2A	dioec.	4–5-fid, ± flat	125–250	non-prol.	confl. (free)	subglobose-depressed	4(–8)-lobed	200†	columnar
T. elliptica	2A	monoec.	4-fid, flat	65–300	non-prol.	free (confl.)	globose-depressed	4-lobed	150–200†	columnar

TABLE 6. Continued.

			Androecious Flower	Stamens			Gynoecious Flower		Styles	
Species	Group	Sex	Shape at Anth.	No. (ca.)	Connective	Loculi	Shape	Orifice	No. (ca.)	Shape
T. leptophylla	2A	monoec.	4-fid, flat	80–90	apic.	free	globose-depressed	circul., entire	300–600	conical
T. madagascariensis	2A	dioec.?	4-fid, flat	200	apic.	free	subglobose-depressed	circul., entire	200†	columnar
T. kirkii	2B	monoec.	3-fid, subglobose	50?	prol.	free	patellif.-urceol.	circul., entire	200	conical
T. paradoxa	2B	dioec.?	globose, with small pore	40–50	prol.	free	?	?	?	?
T. capuronii	3	monoec.	4(–5)-fid, flat	300	prol.	free	napiform-depressed	±6-lobed	200†	conical
T. moheliensis	3	monoec.	4-fid, closed, subglobose	50	prol.	united basally	napiform-depressed	4-lobed	100–200	conical
T. gracilis	4	dioec.?	globose, with small pore	50	non-prol.	confl.	?	?	?	conical
T. purpurea	4	monoec.	globose, with small 3–4-lobed pore	20–32	non-prol.	confl.	globose	small, 3–4-lobed	35–70	columnar
T. religiosa	4	monoec.	closed? 4-lobed	50–75	apic. (non-prol.)	free-conniv.	napiform-depressed	4-lobed	300	conical
T. amplifolia	5	monoec.	4-fid, flat	100–250	non-prol.	confl.	napiform-discoid	4-lobed	300	conical
T. cocottensis	5	monoec.	4–7-fid, flat	150–200	prol.	free	napiform-depressed	5–7-lobed	150–200	setose
T. cordifolia	5	dioec.	4-fid, flat	300–400	non-prol.	free-confl.	napiform-urceolate	4-lobed	100–400	conical

TABLE 6. Continued.

			Androecious Flower	Stamens			Gynoecious Flower		Styles	
Species	Group	Sex	Shape at Anth.	No. (ca.)	Connective	Loculi	Shape	Orifice	No. (ca.)	Shape
T. pedicellata	5	monoec.	4(–6)-fid, half closed	50–70	non-prol.	free	subglobose	4–7-lobed	60–180	conical
T. tau	5	monoec.	4–5-fid, flat	100–150	apic. (non-prol.)	free	subglobose-urceolate	5–10-lobed	80–100	setose
T. tetragona	5	dioec.?	?	?	?	?	napiform-depressed	4-lobed	200	conical
T. bathiei	6	monoec.	3–4-fid, flat	350–450	non-prol.	free-confl.	globose	?	200†	conical
T. sieberi	6	monoec.	(4–)5-fid, flat	100–140	apic. (non-prol.)	free	globose	subcirc., small	850–875	setose
T. perrieri	7	monoec.	4-fid, flat-recurved	150–200	non-prol.	free	obovoid-obpyrif.	4-lobed, small	200	conical
T. quadrifida	7	monoec.	4-fid, flat-recurved	300–500	non-prol.	free	oblong-ellipsoid	3–4-lobed, very small	200–300	conical
T. alaticarpa	8	monoec.	4-fid, flat	38	non-prol.	free	cylindrical	6–8-lobed	250–300	conical
T. longicarpa	8	monoec.	4-fid, flat	40–50	prol.	free	cylindrical	4–6-lobed	500	conical
T. castri-delphinii	9	dioec.?	4–5-fid, flat-recurved	200–300	non-prol.	confl.	napiform-depressed	X-shaped	800–900	conical
T. ficus	9	monoec.	5–7-lobed, urceolate or flat	900–1,800	prol.	free (±unilateral)	urceolate	6–8-lobed	1,000–2,000	setose
T. peltata	9	dioec.	4–5-fid, flat-recurved	200–400	apic. (non-prol.)	free-confl.	discoid	4–7 flat lobes	400–500	flat, columnar (crowded)

is continuous. In *T. purpurea* (Fig. 18E), locular confluence is accompanied by an extreme staminal shortening and broadening, the resulting stamen being sessile or subsessile (0.7–1.2 mm long) with a single, crescentiform loculus which dehisces apically (Endress, 1980b; as *T. religiosa*) as in some species of *Ephippiandra*. However, basal fusion of the loculi occurs only in *T. moheliensis* (Fig. 18D), and also in some (but not all) stamens of *T. cordifolia* (Fig. 42C–E).

Anatomically, the androecious receptacle is similar to that of the gynoecious one. A single vascular bundle supplies each stamen (e.g., in *T. tau*). The same types of idioblasts are often found in the androecious flowers as in the gynoecious ones, most commonly oil and tanniferous cells. Stone cells, however, tend to be less abundant or lacking in the androecious flowers, e.g., *T. purpurea* (Endress, 1980b; as *T. religiosa*). Their greater abundance in gynoecious flowers and fruits suggests they may play a role in protecting the developing ovules from predation.

Floral color is relatively constant in many species, but quite variable in others (Table 8) which often have two color morphs. Flower color is always constant on a given individual and frequently constant within a local population. In *T. quadrifida,* however, both color morphs were observed in a single population at Yemen Valley, Mauritius. Incidentally, floral odor was found to be quite constant for each species and provides a diagnostic field character. Floral morphology, color, and odor all appear to be related to pollination syndromes (see discussion under Floral Biology).

In summary, floral size and morphology, including number, structure, and color of stamens in the androecious flowers and number, structure, and color of the styles in the gynoecious flowers are distinctive for most species of *Tambourissa.* These features provide some of the most taxonomically useful characters in the genus and should be recorded in the field notes. As flowers lose their shape upon drying, supplementary collections of flowers in alcohol should also be made whenever possible, as well as a photographic record. For a more detailed study of the floral morphology and anatomy of *Tambourissa,* see Endress and Lorence (1983).

FRUITING RECEPTACLE AND CARPELS

The seed-like fruiting carpels of all the genera for which information is available are fundamentally similar in being drupaceous and indehiscent with a lignified endocarp, an abundant, oily endosperm, and a small embryo. While much larger in fruit, the shape of the receptacle and the carpels' position largely correspond with their shape and position in flower; i.e., significant generic differences exist. Also, the thick, pitted, bony white endocarp of *Monimia* (Monimioideae sensu Thorne, 1974) differs conspicuously from the thinner, finely sculptured, brownish, horny endocarps of the genera in Mollinedioideae (e.g., *Ephippiandra* and *Tambourissa*; unknown in *Decarydendron*).

Fruiting receptacles of all three species of *Monimia* are similarly subglobose to ovoid, enclosing from one to 12 free, seed-like drupaceous carpels. On herbarium labels these are often mistaken for multiple-seeded fruits. Fruiting receptacles of *Monimia* are strikingly similar to those of *Palmeria* (Corner, 1976; Endress, 1980b). At maturity the receptacle splits longitudinally from the apex into three to six irregular, valvate lobes that open to reveal the bright orange fruiting carpels set against the pinkish red receptacular surface (Figs. 14C, D, 19C). Birds appear to be the effective seed vectors for *M. ovalifolia* in Mauritius (Lorence, pers. observ.), and also for the species of *Monimia* in Réunion (A. Rolland, pers. comm.).

The indehiscent carpels of *Monimia* consist of a lignified, bony endocarp enveloped by a soft, orange, aril-like outer coating apparently composed of two distinct elements. The outermost is an enation extending downward from the stylar base over the apical portion of the carpel and forming a cap-like structure covering the lateral portions of the carpel, while leaving the dorsal and especially the ventral portion exposed (Fig. 19A, B, D). This outgrowth contains numerous oil cells and appears to represent an arilloid structure. The inner layer consists of the mesocarp proper which completely surrounds the endocarp, but is thickest basally (Fig. 19A, B, D). It is also orange but lacks the oil cells of the former. An analogous situation occurs in the neotropical *Siparuna* (Corner, 1976; Endress, 1973), and has been termed a "carpellary aril" or "stylar aril" respectively by these authors. Further studies on the development of *Monimia* carpels are in progress (Endress & Lorence, in prep.).

The endocarp of *Monimia* is whitish, irregularly ovoid-compressed, longitudinally crested and apically mucronate with the micropyle passing through the base of the beak. The wall is hard and bony, ca. 0.5–2 mm thick (probably adequate to survive passage through a bird's gut),

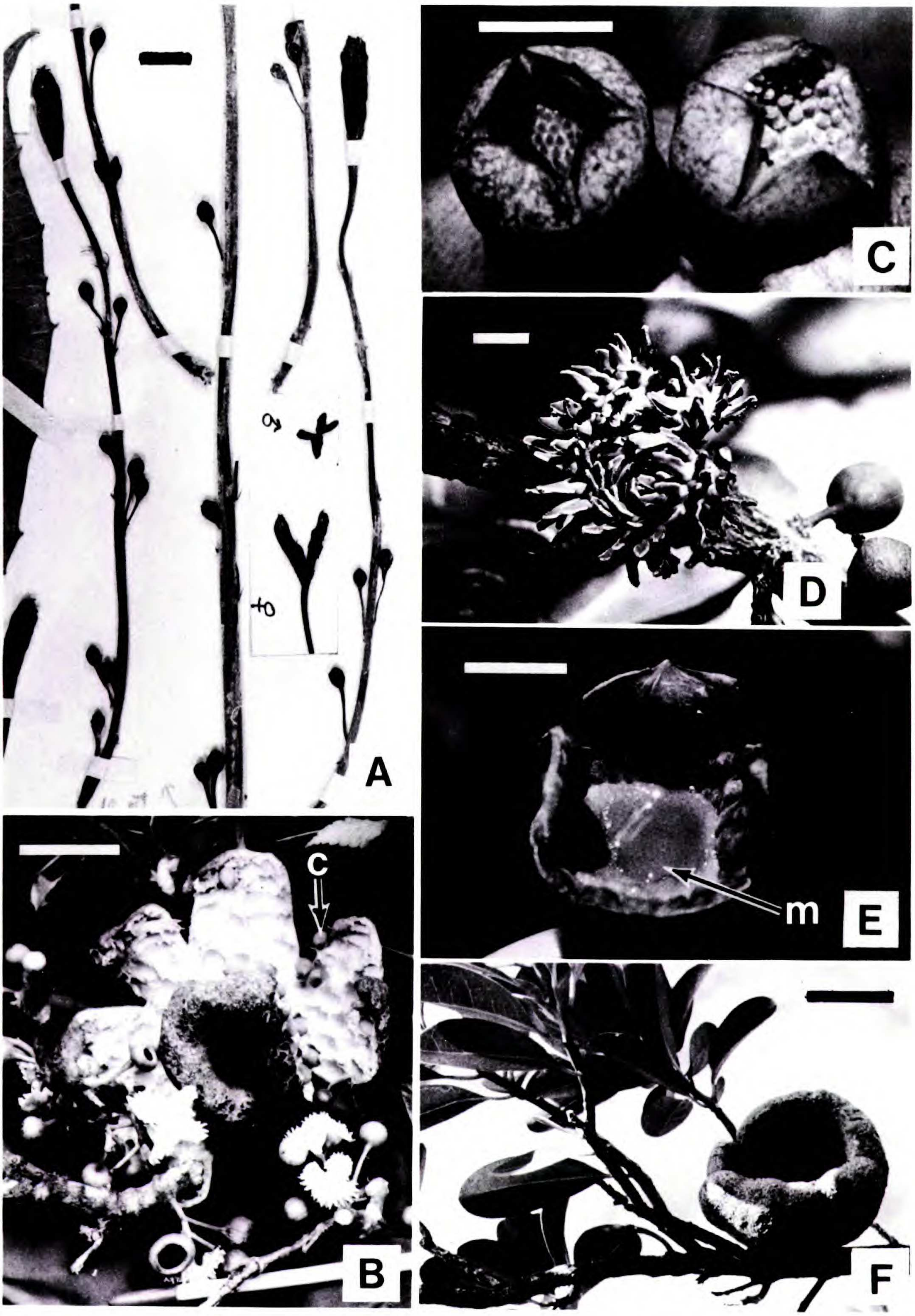


FIGURE 17. Flowers and fruits of some *Tambourissa* species.—A. *T. alaticarpa,* inflorescences showing terminal gynoecious flowers and lateral androecious flowers in bud, inset shows androecious flower at anthesis and longitudinally sectioned gynoecious flower, *Perrier de la Bâthie 10102* (P).—B. *T. comorensis,* inflorescences with androecious and gynoecious flowers, and dehisced fruiting receptacle exposing ripe carpels (c), *Lorence*

TABLE 7. Selected floral anatomical features of *Tambourissa* species according to Group. Data given for both androecious and gynoecious flowers, except where noted. ± indicates presence of a small amount.

Species	Group	Tanniferous Idioblasts	Stone Cells (Sclerids)	Oil Cells	Mucilaginous Compitum (Gynoecious)
T. thouvenotii	1A	+	−	−	−
T. trichophylla	1A	−	+	+	−
T. uapacifolia (♂)	1A	−	−	+	?
T. decaryana	1B	−	+	+	+
T. hildebrandtii	1B	+	−	+	−
T. humbertii	1B	−	−	+	−
T. nitida	1B	+	−	+	?
T. nosybensis	1B	−	+	+	+
T. floricostata	1C	+	−	+	?
T. parvifolia	1C	−	+	+	?
T. beanjadensis	2A	−	+	+	±
T. comorensis	2A	−	+	+	±
T. crassa	2A	−	−	+	+
T. elliptica	2A	±	+	−	+
T. leptophylla	2A	−	+	+	−
T. madagascariensis	2A	+	+	+	±
T. kirkii	2B	?	?	?	− (?)
T. paradoxa (♂)	2B	−	+	+	?
T. capuronii	3	+	+	−	−
T. moheliensis	3	+	+	±	−
T. gracilis (♂)	4	−	−	+	?
T. purpurea	4	+	+	−	+
T. religiosa	4	+	+	−	− (?)
T. amplifolia	5	+	+	+	−
T. cocottensis	5	+	+	−	−
T. cordifolia	5	+	+	−	−
T. pedicellata	5	−	+	+	−
T. tau	5	+	+	+	−
T. tetragona	5	+	−	+	−
T. bathiei	6	+	+	+	−
T. sieberi	6	−	+	+	−
T. perrieri	7	−	+	+	−
T. quadrifida	7	+	+	−	−
T. alaticarpa	8	+	+	−	−
T. longicarpa	8	+	+	+	±
T. castri-delphinii	9	+	+	+	−
T. ficus	9	+	+	+	−
T. peltata	9	+	+	−	+

and consists of many layers of contiguous sclerids. The endocarp surface is externally deeply pitted as in *Peumus* and *Siparuna*. Surface sculpturing ranges from foveate to reticulate or sulcate, varying even within a single species. Inside, a thin single-layered tegmen composed of elongated, rectangular cells encloses the abundant, oily endosperm. The small embryo is situated near the micropyle (Fig. 19A) and has slightly divaricate cotyledons. Germination of both *M.*

←

2870 (MO).—C. *T. pedicellata,* gynoecious (left) and androecious (right) flowers at anthesis, *Lorence 2384* (MO).—D. *T. peltata,* androecious flower at anthesis and two androecious buds, Perrier Nature Reserve, Mauritius (R. E. Vaughan, unvouchered photo).—E. *T. peltata,* newly opened gynoecious flower, note copious mucilaginous exudate (m) on gynoecial disc, *Lorence 2555* (MO).—F. *T. peltata,* submature fruiting receptacle on branch, *Lorence 2197* (MO). Bars equal 10 mm in A, C–E, and 50 mm in B, F.

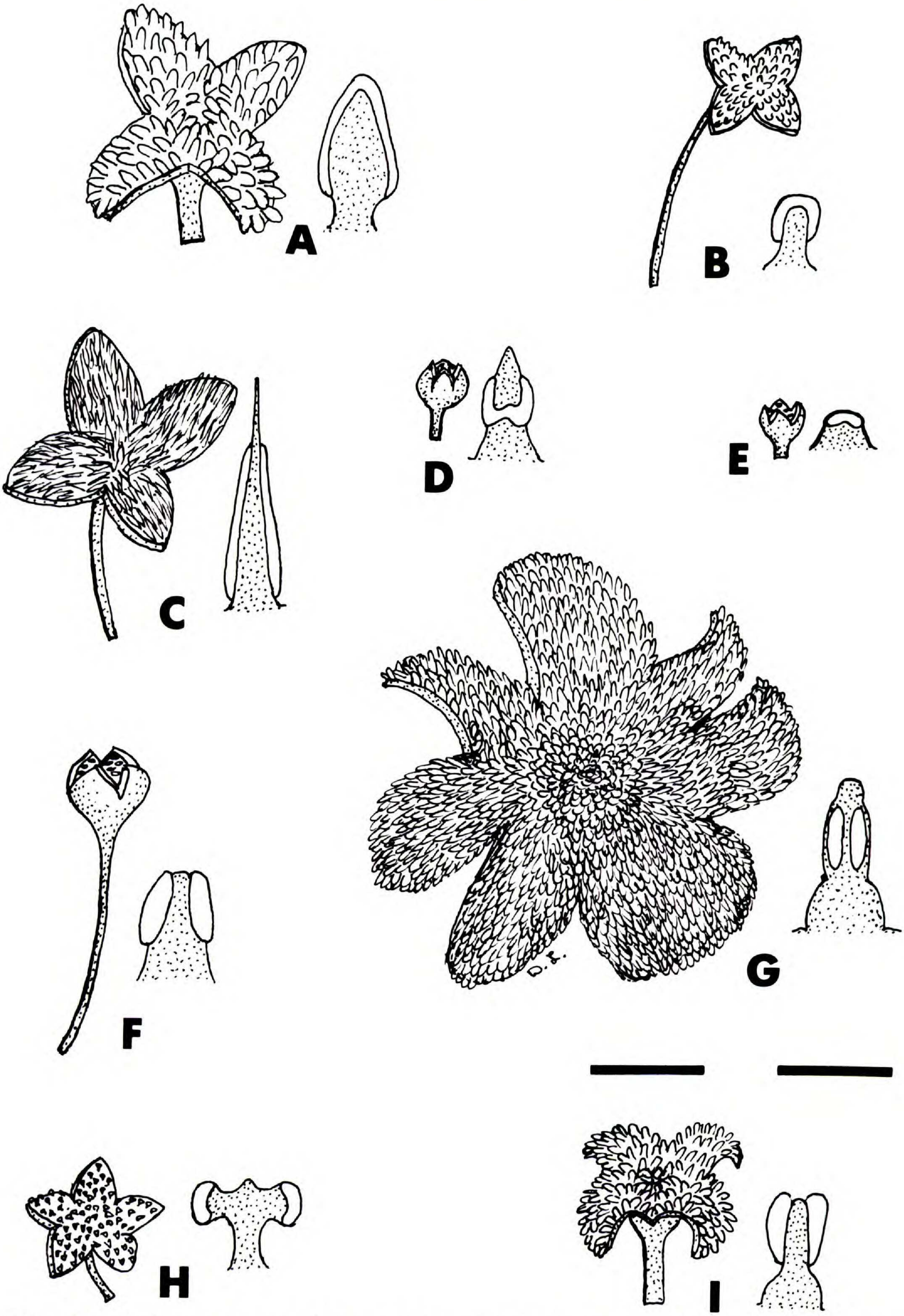


FIGURE 18. Androecious flowers and stamens of some *Tambourissa* species, drawn to approximate scale.—A. *T. peltata.*—B. *T. amplifolia.*—C. *T. capuronii.*—D. *T. moheliensis.*—E. *T. purpurea.*—F. *T. pedicellata.*—G. *T. ficus.*—H. *T. tau.*—I. *T. quadrifida.* Bar equals ca. 10 mm for flowers and ca. 1 mm for stamens.

TABLE 8. Floral color morphs of individuals of some species of *Tambourissa* from Mauritius and Réunion (inner receptacle surface, stamens or styles).

Species	Androecious Flower Color	Gynoecious Flower Color
T. amplifolia	white	orange; pale yellow
T. cordifolia	white	pink; purple-red
T. crassa	pale yellow; dark purple-red	pale yellow-green; dark purple-red
T. elliptica subsp. *elliptica*	white; pink	pale yellow-green; pink
T. ficus	white; purple-red	yellow-pink
T. peltata	purple-red; salmon pink	lobes purple-red, disc orange
T. quadrifida	orange; red	greenish white; reddish pink
T. sieberi	pale yellow; purple-red	pale yellow-green; purple-red
T. tau	greenish white; purple-red	purple-red

ovalifolia and *M. rotundifolia* seeds took over four months and viability was quite low, ca. 10–15%.

Fruiting carpels of *Decarydendron* are unknown (Cavaco, 1959). Because its flowering carpels are free and subsessile on the receptacular surface, the fruiting carpels may resemble those of *Ephippiandra* in being free and exposed on the receptacle, but probably lack a basal cupule and are sessile or shortly stalked as in *Hedycarya* or *Mollinedia*.

Mature fruiting receptacles of *Ephippiandra* (including *Hedycaryopsis*) are discoid, flat to convex, fleshy and red when fresh, and bear ca. 10–75 free, ovoid to ellipsoid carpels ca. 7–12 mm long. Each is partly surrounded basally for about one-third to one-half its length by a cupule (Fig. 14H) derived from the receptacle. The mature carpels are composed of a thin, fleshy green exocarp which turns black on ripening and surrounds the thin, pale brown, horny endocarp. The endocarp surface is smooth and finely scrobiculate as in *Tambourissa* and encloses a copious, fleshy endosperm.

As in the other genera, fruiting receptacles of *Tambourissa* (including *Phanerogonocarpus*) are many times larger than the flowers but otherwise similar in shape, ranging from flat and discoid (e.g., some *T. peltata* fruits), or somewhat open and cupuliform in the majority (e.g., Figs. 17B, F, 42J), to ellipsoid and closed with a small orifice in *T. quadrifida*, or cylindrical with four to five prominent external ridges in *T. alaticarpa* and *T. longicarpa*. The majority are corky brown externally, but may be smooth and dark (reddish when fresh) in *T. purpurea* and *T. religiosa*. Most have an internal cavity, but some fruits of *T. hildebrandtii* are almost solid. The styles persist in fruit and line the cavity, providing important diagnostic features as to their size, shape, and number. Other taxonomically useful features of the fruiting receptacle are its position on the plant (on the trunk, branches, or terminal), whether solitary or in clusters, its size, shape, and the proportional size of the orifice.

At maturity the receptacle splits open irregularly, exposing the numerous, bright red-orange

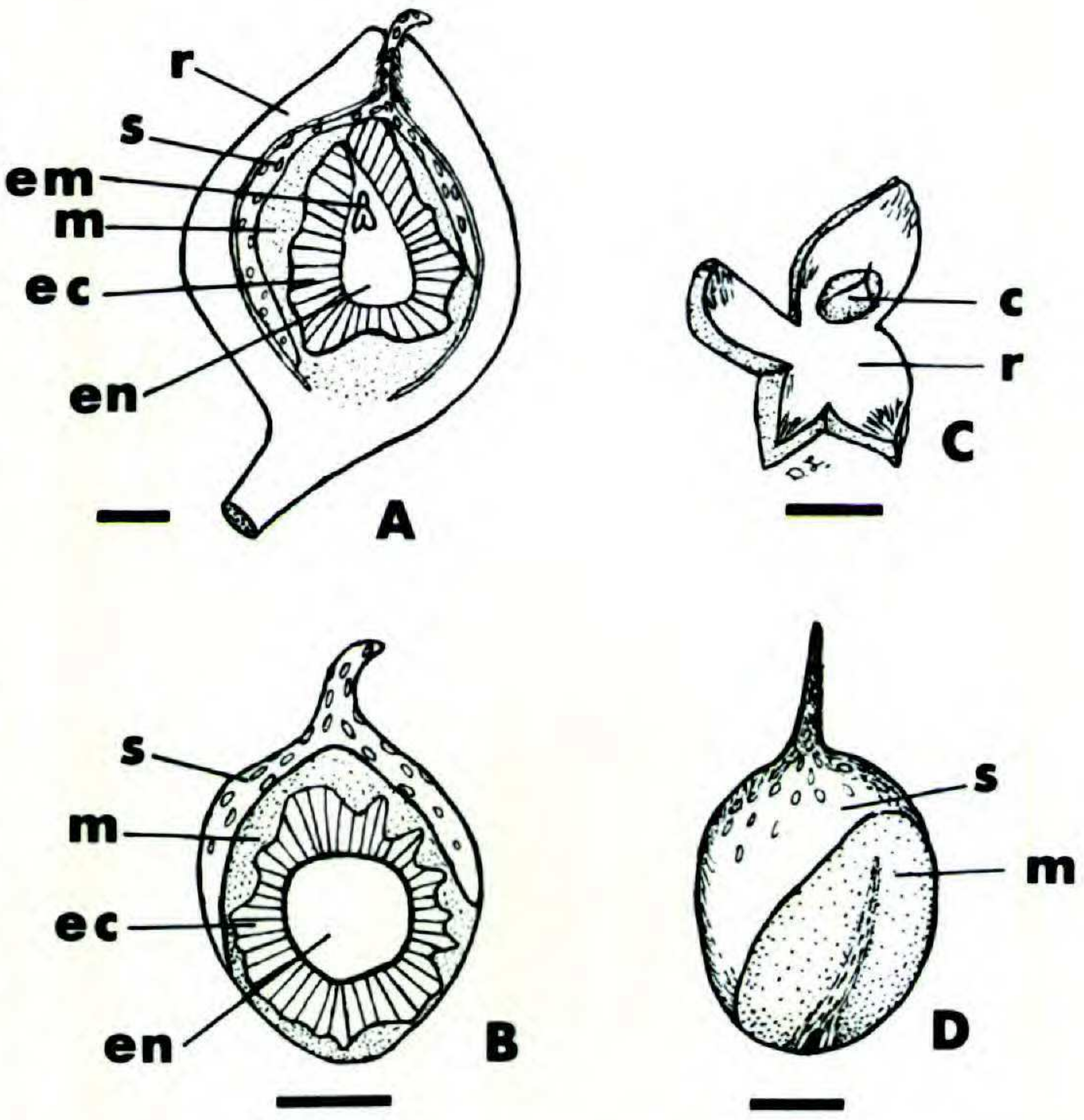


FIGURE 19. *Monimia* fruiting receptacles and carpels.—A. *M. ovalifolia,* submature fruiting receptacle with single carpel, longitudinal section, *Lorence 2350* (MO).—B. *M. ovalifolia,* mature fruiting carpel, longitudinal section, *Lorence 2350* (MO).—C. *M. amplexicaulis,* ripe receptacle split open to reveal single carpel, *Lorence 2503* (MO).—D. *M. amplexicaulis,* ripe fruiting carpel, abaxial view, *Lorence 2503* (MO). Bars equal 2 mm in A, B, D, and 10 mm in C. c = carpel; ec = endocarp; em = embryo; en = endosperm; m = mesocarp; r = receptacle; s = stylar aril.

carpels which separate from the pale orange receptacular ground tissue (Fig. 17C). In *Tambourissa cordifolia* (*Lorence 2630*, MO), the receptacle consists of parenchymatous ground tissue intermixed with sheets and columns of tanniferous cells and brachysclerids comprising nearly half the total tissue mass. In carpels of *T. cordifolia* the mesocarp is composed of parenchymatous cells containing numerous orange plastids interspersed with abundant oil cells and has a sweet taste when fresh (D. Lorence, pers. observ.). Beneath the mesocarp lies a horny, brown endocarp with a smooth, finely sculptured surface composed of numerous subspheroidal to cuboidal, lignified sclerids united into longitudinal bands and overlain by a single outer layer of flat, discoid sclerids. Beneath this lies an endotesta of elongated, annular tracheids three to four cell layers thick, and finally a unicellular tegmen of cuboidal cells surrounding the abundant endosperm whose cells are full of oil droplets. The embryo is 3–4 mm long, situated apically near the micropyle, and has two flat, erect cotyledons.

Carpels of various species differ somewhat in size and also color and sculpturing of the endocarp. In three Mauritian species belonging to Group 5 (i.e., *Tambourissa amplifolia, T. pedicellata,* and *T. tau*), it has sparsely branched, longitudinal ridges. Otherwise the carpels provide few taxonomically useful characters. Birds appear to be the effective seed vectors in *Tambourissa* (D. Lorence, pers. observ.; A. Rolland, pers. comm.; *Benson 142,* BM).

In summary, morphological and anatomical features of the wood, stems and phyllotaxy, leaves, inflorescence, flowers, and fruits of the Malagasy Monimiaceae often display marked trends and provide important diagnostic characters at the generic level. Furthermore, features of trichomes, inflorescence, and in particular floral morphology and anatomy also provide valuable diagnostic features at the specific level.

POLLEN

As a detailed palynological study of the Malagasy Monimiaceae has been published elsewhere (Lorence et al., 1984), only a brief summary of the results will be given here.

The four genera studied here all possess inaperturate spheroid, subspheroid, or ovoid pollen characteristic of the majority of the Monimiaceae sensu stricto excluding the Atherospermoideae, whose pollen is disulcate (Money et al., 1950; Walker, 1976). Although Walker (1976) probably meant to exclude the spinose pollen of *Monimia* (Monimioideae), his statement that pollen of "... most of the genera on Madagascar and the Mascarenes is distinctive in possessing spiral bands on the surface" in the manner of *Hortonia* (Hortonioideae; Ceylon) does not accurately describe the pollen of the other three genera (all Mollinedioideae). Their sexines exhibit variable patterns ranging from spinose in *Monimia,* corrugate in *Decarydendron,* either granulate, reticulate, striato-rugulate, striato-reticulate, or tectate in *Tambourissa* (including *Phanerogonocarpus*), to granulate with verrucate, gemmate, or even vesiculate processes in *Ephippiandra* (including *Hedycaryopsis*) (Lorence et al., 1984).

It was found that pollen size, exine thickness, and sexinous patterns appear to provide useful, species-specific characters in the majority of species examined in this study. Although palynological evidence does not support the segregation of *Hedycaryopsis* from *Ephippiandra,* nor of *Phanerogonocarpus* from *Tambourissa,* generic differences in pollen are otherwise distinctive.

CHROMOSOME NUMBERS

As chromosome numbers provide some degree of support for the segregation of at least some of the subfamilies of Monimiaceae (e.g., Ehrendorfer et al., 1968; Goldblatt, 1974), and because all of the genera in the Malagasy region were previously unknown cytologically, it was decided to accumulate as much chromosomal information as possible during this study. All the reported counts were obtained from androecious flower buds fixed in 3 : 1 absolute ethanol : glacial acetic acid and later examined by the acetocarmine squash method.

Chromosomal study of all three species of *Monimia* has proven extremely difficult because of their small size and high number, a difficulty compounded by their tendency to stick together and by the presence of cytoplasmic inclusions. As a result, only approximate counts were obtained, both for *Monimia rotundifolia*: Réunion, Bébour cloud forest, *Lorence 2429* (MO), $n =$ ca. 44; Réunion, Col de Bellevue, cloud forest, *Lorence 2473* (MO), $n =$ ca. 48. The gametic chromosome number for this species therefore lies somewhere between 40 and 50, and it is obviously paleopolyploid.

These chromosomal findings for *Monimia* do not appear to suggest any close numerical affinity with *Peumus* ($2n = 78$; Morawetz, 1981). Both genera appear to be polyploids, however, as opposed to the majority of Monimiaceae sensu stricto (P. Goldblatt, pers. comm.).

All nine species of *Tambourissa* examined cytologically in this investigation had a gametic chromosome number of $n = 19$ (Table 9).

Although six of the species were from Mauritius, a few from Grande Comore, Réunion, and Madagascar were also examined with the same results. This suggests that the extensive adaptive radiation of *Tambourissa* in the Malagasy region has occurred at the same chromosomal level.

The paleohexaploid base number $x = 19$ (Goldblatt, 1980) is shared with a number of genera from Oceania also belonging to Mollinedioideae sensu Thorne (1974)—i.e., *Hedycarya, Levieria, Palmeria,* and *Wilkiea* (Ehrendorfer et al., 1968)—as well as by *Hortonia* in the Hortonioideae (Goldblatt, 1974). As in *Tambourissa,* these genera are characterized by androecious flowers bearing numerous, irregularly spaced subsessile stamens with lateral dehiscence (Ehrendorfer et al., 1968), although gynoecious floral construction is more variable (Endress, 1980b). Similarities in cytology and androecious floral morphology among these genera suggest they are relatively closely allied within the Mollinedioideae.

The remaining endemic Madagascan genera belonging to the Mollinedioideae—i.e., *Decarydendron* and *Ephippiandra* (including *Hedycaryopsis*) as well as both *Tambourissa* species formerly included in *Phanerogonocarpus*—are unknown cytologically.

Floral Biology

Although the vegetative and floral anatomy (Money et al., 1950), palynology (Walker, 1976), and cytology (Ehrendorfer et al., 1968; Goldblatt, 1974) of various extant primitive angiosperm families have been relatively well studied, comparatively little is known of their floral biology and breeding systems. I have therefore attempted to accumulate as much data as possible on these aspects of the Monimiaceae while in the Malagasy area.

The only confirmed report on pollination in Monimiaceae sensu stricto is by Gottsberger (1977), who observed female thrips making holes and ovipositing in androecious and gynoecious flower buds of *Mollinedia* in Brazil. The larvae develop and mature inside the buds and the adults emerge as the buds open, flying out and carrying pollen to other flowers as they seek mates. Endress (1979, 1980b) also reported finding holes and eggs in flowers of *Wilkiea* and *Stegnanthera* (Mollinedioideae), which may have been from pollinating insects. More recently, investigations by Thien (1980) on the pollination of species of primitive angiosperms belonging to the Degeneriaceae (*Degeneria*) and Winteraceae (*Drimys, Belliolum,* and *Zygogynum*) in the South Pacific islands show that members of the orders Coleoptera, Diptera, Lepidoptera, and Thysanoptera are important pollinators of these plants.

The present study was conducted in Mauritius during 1978–1979 and includes observations on seven species of *Tambourissa* and one species of *Monimia.* The species studied, study sites, and observation periods are given in Tables 10 and 11. Insect visitors were captured, killed, and mounted or stored in 70% alcohol for identification. Flowers of all species studied were observed and photographed during various stages. Voucher specimens of the plants are deposited at MAU and MO.

Tambourissa is a genus of monoecious or dioecious shrubs, treelets, or trees. All species have highly specialized, unisexual flowers with minute, scale-like tepals, a well-developed receptacle which assumes the functions of a perianth and ovary wall, and inferior carpels. As an understanding of the floral morphology is essential to understand the pollination biology, this chapter should be read in conjunction with the section on floral morphology and anatomy.

Female receptacles of most species are somewhat globose and closed in bud, and split open at maturity into (3–)4–5(–10) lobes, depending on the species. Once open, they do not close again. The receptacle is lined with numerous short to long styles, each corresponding to a single carpel. These become receptive gradually and centripetally during floral anthesis, which typically lasts 10–15 days. Receptive styles of most species produce a slight mucilaginous exudate in which the pollen tubes germinate and grow (e.g., *Tambourissa tau, T. cordifolia,* Figs. 13E, 16C). In others, the styles are reduced and covered by a massive mucilaginous secretion (compitum) (e.g., *T. peltata,* Fig. 17E). In yet others (e.g., *T. purpurea*), the flower remains closed except for a mucilaginous plug which occludes the floral entrance and has a stigmatic function (Endress,

TABLE 9. Collections of *Tambourissa* in which the haploid chromosome number was determined as $n = 19$. All collections are mine; vouchers are deposited at MO and most at MAU also.

Species	*Lorence* Number	Locality
T. comorensis	*2878*	Grande Comore. La Grille, wet forest.
T. cordifolia	*2571*	Mauritius. Pétrin Nature Reserve, *Philippia* heath formation.
T. elliptica		
subsp. *elliptica*	*2526, 2530*	Réunion. Takamaka, wet forest.
subsp. *micrantha*	*2483*	Réunion. Mare Longue, wet forest.
T. pedicellata	*2384*	Mauritius. Pieter Both Mt., degraded wet forest.
T. peltata	*2553*	Mauritius. Cascade Alexandra, stunted wet forest.
T. purpurea	*1726*	Madagascar. Wild, locality unknown (cult. MO).
T. quadrifida	*2539*	Mauritius. Matala Valley (Yemen), semideciduous dry forest.
T. sieberi	*2250*	Mauritius. Mt. Cocotte Nature Reserve, cloud forest.
T. tau	*1964*	Mauritius. Piton de la Rivière Noire, wet forest.
T. tau	*2951*	Mauritius. Perrier Nature Reserve, wet forest.

1979, 1980b; as *T. religiosa*). This "hyperstigma" occurs in some Madagascan and Réunion species, but is absent from Mauritian and Comorean plants. The sweet mucilage of *T. purpurea* tested positive for reducing sugars with Benedict's solution and for glucose with Lilly TES-tape (paper for analysis of urine sugar), respectively (Endress & Lorence, 1983). It therefore probably has a nectar function in a number of species that produce an abundant secretion (e.g., *T. crassa, T. elliptica, T. peltata, T. purpurea*). Flowers of most Mauritian species also produced strong floral odors which presumably attract pollinators.

Androecious flowers are similarly lined with numerous stamens that also mature gradually and centripetally after the globose receptacle splits into (3–)4–5(–7) subequal valvate segments. Although a few Comorean and Madagascan species open by a small apical orifice, lobes of most species open flat or even recurve and remain permanently open during their 7–12 day life span. Androecious flowers produce large amounts of pollen, which represent a substantial floral reward, although secretions are absent. In addition, floral odors like those in the gynoecious flowers are emitted.

In the Mauritian *Tambourissa* species, from one to more than 100 flowers were found to be open on a given day, depending on the species and individual, and flowering generally occurred over a three to five month period. These aspects will be discussed below in more detail by species. A synopsis of the results of this study for *Tambourissa* in Mauritius is as follows.

1. Major pollinators are insects belonging to the orders Coleoptera and Diptera.
2. Gynoecious floral morphology, notably size of the floral entrance, plays a key role in regulating insect entry.
3. Floral odor, and possibly also color, plays an important role in attracting pollinators.
4. Floral reward in the androecious flower is pollen. Gynoecious flowers of some species attract by deceit, while in others a mucilaginous exudate seems to have a nectar function.
5. Demography, phenology, and breeding systems are related to pollinator syndromes.

TAMBOURISSA SIEBERI

Tambourissa sieberi, a large, monoecious canopy tree 8–10 m tall, is known from only a few restricted areas of mature wet and cloud forest in Mauritius. It is scarce and occurs as scattered individuals in low population densities, e.g., at Macabé forest (Table 4), and at Mt. Cocotte where it was studied (Table 10). Hundreds of flowers (16–90 per inflorescence) are produced in unisexual pleiochasia and thyrses arising in large numbers from the trunk and major branches from December to February.

Gynoecious flowers are globose with a small apical pore only 2–3 mm diam. (Fig. 20A). Several hundred long styles which are coalescent into groups fill the receptacle, leaving only a small central cavity (Fig. 15E). The styles are moist at anthesis due to a slight surface exudate. Androecious flowers are relatively large and split into five spreading, reflexed lobes bearing ca. 100–

TABLE 10. Localities for pollination biology studies in Mauritius.

No.	Locality	Vegetation Type	Elevation (m)	Annual Pptn. (mm)	Date	Season
1.	Mt. Cocotte	cloud forest	760	5,000	Jan. 1979	wet
2.	Matala valley (Yemen)	semideciduous dry forest	200	1,600	June–July 1979	dry
3.	Perrier	*Sideroxylon* lower montane wet forest	600	3,400	Sept.–Oct. 1978 Sept. 1979 Apr. 1979	dry dry end wet
4.	Pétrin	*Philippia* heath formation	630	4,000	May 1979	start dry
5.	Bel Ombre	Lowland wet (high) forest	300	2,400	Dec. 1978–Jan. 1979	wet
6.	Mare Longue Plateau	Lower montane wet forest	660	3,400	Apr. 1979	end wet
7.	Piton Brise Fer	Lower montane wet forest	700	2,400	Dec. 1978	wet

140 large stamens that release abundant, coalescent pollen. Flowers may be either pale yellow or dark reddish purple, depending on the individual. Flowers of both sexes produce the same strong, cloying odor of overripe or fermenting fruit.

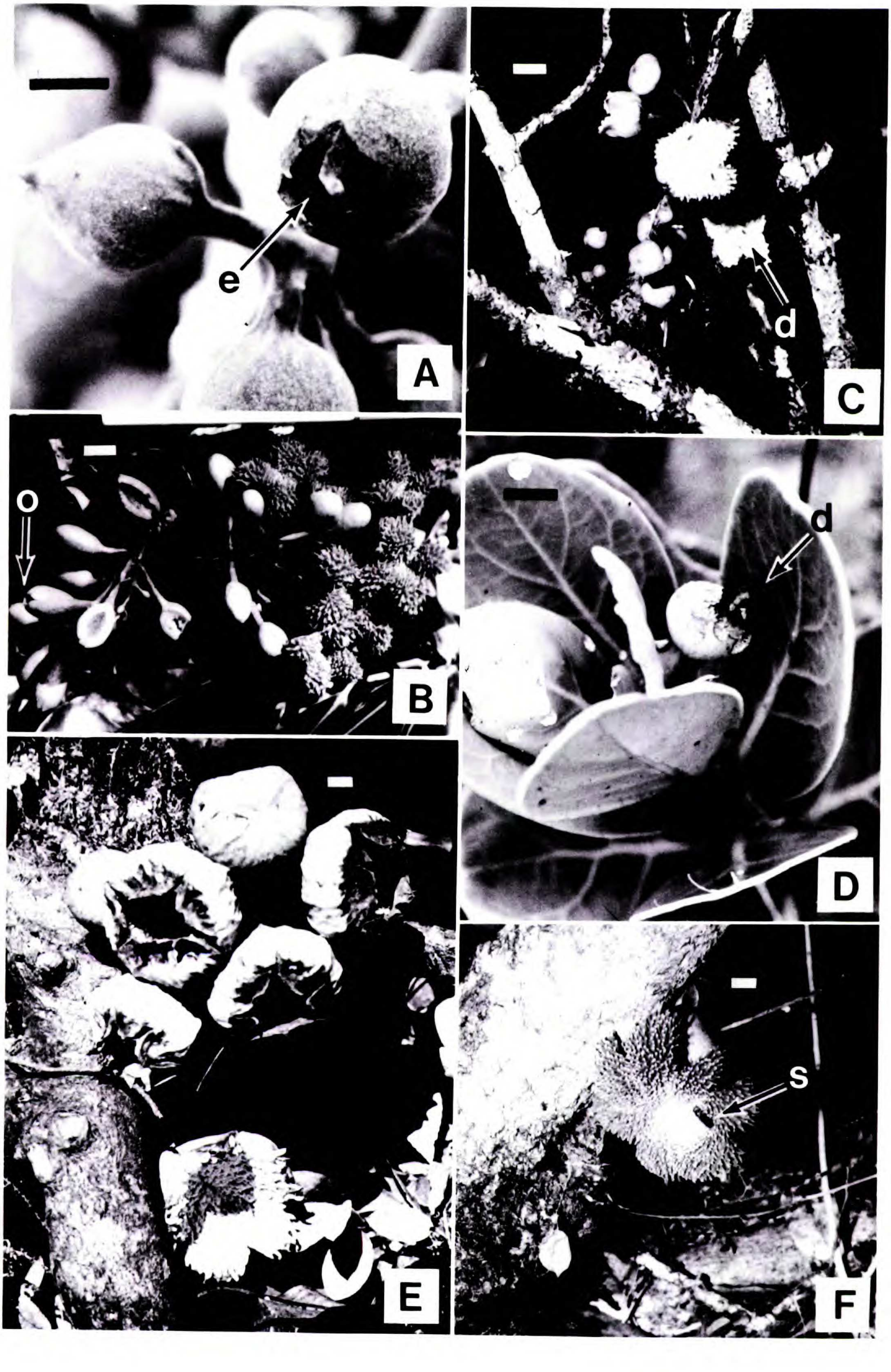
Observations made near midday, totalling 3.4 hours, revealed that introduced honeybees (*Apis mellifera*) were the most frequent visitors of androecious flowers, from which they gathered pollen. They showed no interest in the gynoecious flowers, however, nor could they enter them. Other less frequent visitors to the androecious flowers were unidentified Syrphidae (two species) and another unidentified dipteran (Table 11). No visitors were observed on the gynoecious flowers during this time, and no observations were made at night.

Examination of the contents of ten gynoecious flowers from the tree and 15 fallen flowers revealed the presence of various small arthropods, notably a variety of small Coleoptera only 2–3 mm long, in over half the flowers (Table 12). These Coleoptera, belonging to the families Hydrophilidae, Nitidulidae, Rhizophagidae, and Staphylinidae, are presumably active at night. They probably visit androecious flowers to feed on the pollen, attracted by the strong floral odors. They also enter the gynoecious flowers to feed on the styles, which were damaged in certain flowers, and probably oviposit there, as eggs and larvae were found in some flowers (Table 12). Because the stylar canal is situated near the style's base, damage to its terminal portion probably has little if any effect on pollen tube germination and growth which may occur anywhere on the stylar surface. Reduction of the floral entrance can be viewed as a strategy to protect the ovules from damage by larger, more destructive beetles (cf. Gottsberger, 1974, 1977; Endress, 1980b), at the same time allowing access to the less destructive small beetles. Elongation and coalescence of the styles may provide food for the coleopterans and also protect the ovules. Carpel group formation of this type, by connivence of the styles and cohesion by the mucilaginous secretion, functionally divides the gynoecium into several subunits, each being composed of a number of carpels (Endress & Lorence, 1983). This phenomenon is unknown elsewhere among the angiosperms.

Breeding experiments suggest that *Tambourissa sieberi* is the only self-compatible monoecious species of the four tested in Mauritius (Table 13). I suspect self-compatibility in *T. sieberi* may be a strategy to offset its low population densities and probable inefficiency of the small pollinators. Production of a large number of flowers and a prolonged flowering period may also compensate for these factors.

TAMBOURISSA QUADRIFIDA

Tambourissa quadrifida is the only species of Monimiaceae to occur in the dry forest zone of Mauritius. A mid stratum or subcanopy tree, it occurs in small, scattered populations and readily forms multiple coppice stems. Individuals are subdioecious, producing flowers of predominantly one sex, and flower from June to August. The numerous flowers are produced in pleiochasia and thyrses along the trunk, and hundreds of flowers may be open on a given day, each persisting for ca. 10–15 days. During the 1979 flowering season, a predominantly androecious tree (*Lorence 2656*, MO) was estimated to produce nearly 24,000 flowers, and a predominantly gyn-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oecious tree (*Lorence 2655,* MO) over 15,000 flowers! Crossing experiments carried out on three individuals showed them all to be self-incompatible (Table 13).

The gynoecious flowers of *Tambourissa quadrifida* are ellipsoid to obovoid and open by a small apical pore only 1–2 mm diam. (Fig. 20B). Inside, 200–300 short, glistening pink or yellow styles line the hollow receptacle; only a small amount of stylar exudate is produced. The orange or red androecious flowers split into four ultimately recurved segments bearing 300–500 stamens with slightly coalescent pollen (Fig. 20B). A strong, pleasant odor of ripe fruit is produced by flowers of both sexes.

Studies were carried out on a population of four individuals at Yemen (Matala Valley) on the edge of a dry forest degraded by numerous exotics. Observations totalling 13.4 hours revealed that large numbers of small Diptera (*Drosophila* spp., *Homoneura,* and *Zaprionus*) congregated on the androecious flowers in the early morning, but did not enter the gynoecious flowers (Table 11). For this reason, the drosophilids presumably have little, if any, effect as pollinators. Three species of syrphids also visited the androecious flowers occasionally during the day to feed on the pollen, and pollen foraging activity by honeybees was also intense throughout the day. As these insects are all too large to enter the gynoecious flowers in which the styles are concealed, they cannot function as pollinators.

An examination of 438 gynoecious flowers from the tree and 132 fallen flowers revealed that 93.6% and 75.8% respectively were devoid of any contents (Table 14). A number contained mealybugs which were presumably brought in by the small ants also found in some flowers. Ants are probably ineffective as pollinators, as they did not visit androecious flowers. A small percentage of flowers contained silk webbing, often with small larvae or pupae (probably Lepidoptera). These larvae appeared to graze on the styles and probably represent predators, although pollinating activity by the ovipositing adults cannot be discounted. The only likely pollinator observed was a small Nitidulidae beetle, *Haptoncus luteolus* (Tables 11, 14) seen emerging from a gynoecious flower. It subsequently visited an androecious flower to forage for pollen, which adhered to its body. The beetle is probably able to travel the short distances of several meters separating trees in this population. Significantly, another species of *Haptoncus* was seen in the structurally similar gynoecious flowers of *Tambourissa sieberi* (Table 12), and Thien (1980) found the same genus in *Degeneria* flowers.

One factor responsible for the scarcity of pollinators on *Tambourissa quadrifida* at Yemen may have been the disturbed, partly secondary nature of the habitat. However, the predominantly gynoecious tree of the four usually produces some fruit clusters each year (J. A. Lalouette, pers. comm.), indicating that effective cross pollination does occur to a certain degree.

As in *Tambourissa sieberi,* an extreme reduction of the gynoecious floral entrance excludes larger, more destructive insects, permitting only smaller pollinators like the nitidulid to enter. The tremendous floral production in *T. quadrifida* presumably offsets the lower efficiency of these insects as pollinators as in *T. sieberi,* whereas self-incompatibility and subdioecy would enforce outcrossing.

TAMBOURISSA TAU

Tambourissa tau is a slender, monoecious understory treelet rarely exceeding 2–3 m high. Flowers are produced from meristematic swellings along the main stem, or in the leaf axils. Depending on its size, each plant may produce over 100 solitary or fasciculate flowers over a three to five month period, but only several open at a time, each lasting for 10–15 days. Crossing experiments revealed it to be self-sterile (Table 13).

Gynoecious flowers are relatively small, externally corky, and split about half way open into 6–10 irregular, suberect lobes (Fig. 39E, F). Each

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FIGURE 20. Flowers of some *Tambourissa* species.—A. *T. sieberi,* gynoecious flowers in bud (left) and at anthesis (right), note insect egg (e) in orifice, *Lorence 2250* (MO).—B. *T. quadrifida,* inflorescences with gynoecious flowers (left), note small orifice (o), and androecious flowers (right), *Lorence 2656* (MO).—C. *T. cordifolia,* androecious plant with flowers in bud and at anthesis, note visiting drosophilids (d), *Lorence 2632* (MO).—D. *T. crassa,* gynoecious flower at anthesis, note visiting dipteran (d) drinking mucilage, *Lorence 2468* (MO).—E. *T. ficus,* form with partly closed white androecious flowers in bud, at anthesis and post anthesis, *Lorence 1485* (MO).—F. *T. ficus,* form with open purple androecious flower at anthesis, note visiting syrphid (s), *Lorence 2115* (MO). Bars equal 10 mm.

TABLE 11. Pollination biological data for species of Monimiaceae in Mauritius.

Species	Loc.	Date	Time	Weather	T° (C)	Total Obs. Time (hr.)	Insect Visitors/Pollinators	Max. Obs.	No. Flowers Observed
Monimia ovalifolia	1	10 Aug. 1979	11:30 A.M.–1:40 P.M.	cloudy, rainy	16–17.5	2.2	Diptera		
							Syrphidae		
							cf. *Isciodon* sp.	5	numerous
Tambourissa amplifolia	5	10 Jan. 1979	9:10 A.M.–1:40 P.M.	sunny to rainy	26–30	4.5	Diptera		
							Drosophilidae		
							Drosophila cf. *nasuta*	1	6 ♀, 18 ♂
							Lauxaniidae		
							Homoneura sp.	3	6 ♀, 18 ♂
T. cordifolia	4	12 May 1979	1:20 P.M.–5:30 P.M.	sunny to rainy	26–22	4.2	none	0	9 ♂
	4	13 May 1979	6:30 A.M.–11:30 A.M.	dawn to sunny & windy	18–26.5	5.0	Diptera		
							Drosophilidae		
							Drosophila nasuta	total 72	9 ♂
							Zaprionus vittager		9 ♂
	4	13 May 1979	6:45 A.M.–11:10 A.M.	dawn to sunny & windy	18–26.5	4.4	Diptera		
							Drosophilidae		
							Drosophila nasuta	total 12	6 ♀
							Lauxaniidae		
							Pachycerina sp.		6 ♀
	4	19 May 1979	5:00 P.M.–6:45 P.M.	sunny & windy to dusk	19.5–16	1.8	Diptera		
							Drosophilidae		
							Drosophila nasuta	1	7 ♂
	4	30 May 1979	6:05 A.M.–9:05 A.M.	dawn to sunny & windy	18–26	3.0	Diptera		
							Drosophilidae		
							Zaprionus vittager	total 12	6 ♂
							Lauxaniidae		
							Homoneura sp.		6 ♂
	4	30 May 1979	6:45 A.M.–11:15 A.M.	dawn to sunny & windy	19–26	4.5	Diptera		
							Drosophilidae		
							Drosophila nasuta	1	6 ♀

Table 11. Continued.

Species	Loc.	Date	Time	Weather	T° (C)	Total Obs. Time (hr.)	Insect Visitors/Pollinators	Max. Obs.	No. Flowers Observed
Tambourissa ficus	7	8 Dec. 1978	11:00 A.M.–11:50 A.M.	fair	23.5–25	0.8	Diptera		
							Syrphidae		
							Eumerus sp.	2	2 ♂
	1	12 Dec. 1978	8:45 A.M.	fair	—	spot check	Coleoptera		
							Hydrophilidae		
							Cercyon sp.	42	2 ♀, 1 ♂
T. peltata	6	10 Apr. 1979	7:30 A.M.–11:30 A.M.	fair & occ. rain	20–27	4.0	Diptera		
							Drosophilidae (unidentified)	4	16 ♀
							Syrphidae		
							cf. *Askarina*	1	16 ♀
							Diptera (unidentified)	1	16 ♀
	6	19 Apr. 1979	3:45 P.M.–5:30 P.M.	fair, sunny	25–21	1.8	Diptera		
							Syrphidae (unidentified)	1	12 ♀
	3	9 Apr. 1979	10:30 A.M.–10:50 A.M.	fair	24–25	0.3	Diptera		
							Syrphidae		
							Askarina sp.	3	6 ♂
							Hymenoptera		
							Apidae		
							Apis mellifera	1	6 ♂
	3	9 May 1979	11:00 A.M.–11:20 A.M.	fair	25	0.3	Diptera (small, unidentified)	3	2 ♀
	3	10 May 1979	3:45 P.M.–4:00 P.M.	fair	28.5–27	0.3	Diptera (small, unidentified)	1	2 ♀
	3	11 May 1979	3:20 P.M.–4:00 P.M.	fair	28–24.5	0.7	Hymenoptera		
							Apidae		
							Apis mellifera	3	8 ♂
	3	12 May 1979	8:15 A.M.–9:00 A.M.	passing showers	22–23	0.8	Diptera		
							Drosophilidae		
							Drosophila		
							(*melanogaster* grp.)	many	25 ♂
							D. nasuta	many	25 ♂
							Zaprionus hibernaculatus	many	25 ♂
							Syrphidae		
							Askarina sp.	1	25 ♂
							Ornida obesa	2	25 ♂

TABLE 11. Continued.

Species	Loc.	Date	Time	Weather	T° (C)	Total Obs. Time (hr.)	Insect Visitors/Pollinators	Max. Obs.	No. Flowers Observed
Tambourissa quadrifida	2	20 June 1979	7:12 A.M.–11:40 A.M.	fair to cloudy	20–24.5	4.5	Diptera		
							Drosophilidae		
							Drosophila sp.	several	hundreds ♂
							Zaprionus sp.	1	hundreds ♂
							Syrphidae		
							Ornida obesa	1	hundreds ♂
							Hymenoptera		
							Apidae		
							Apis mellifera	5	hundreds ♂
	2	21 June 1979	7:20 A.M.–11:45 A.M.	fair to cloudy	20–24	4.4	Diptera		
							Lauxaniidae (unidentified)	1	several ♂
							Syrphidae (unidentified)	1	several ♂
	2	22 June 1979	7:00 A.M.–11:30 A.M.	fair to cloudy	19.5–24	4.5	Diptera		
							Drosophilidae		
							Drosophila nasuta	many	hundreds ♂
							D. (*melanogaster* grp.)	many	hundreds ♂
							Zaprionus sp.	2	hundreds ♂
							Lauxaniidae		
							Homoneura quadrivittata	3	hundreds ♂
							Syrphidae (2 spp., unident.)	3	hundreds ♂
							Coleoptera		
							Nitidulidae		
							Haptoncus luteolus	1	1 ♀
							Hymenoptera		
							Apidae		
							Apis mellifera	6	hundreds ♂
T. sieberi	1	4 Jan. 1979	11:00 A.M.–12:12 P.M.	fair to cloudy	28–29	1.2	Hymenoptera		
							Apidae		
							Apis mellifera	6	many ♂

TABLE 11. Continued.

Species	Loc.	Date	Time	Weather	T° (C)	Total Obs. Time (hr.)	Insect Visitors/Pollinators	Max. Obs.	No. Flowers Observed
	1	4 Jan. 1979	12.45 P.M.– 1:55 P.M.	fair to cloudy	25.5– 24	1.2	Diptera		
							Syrphidae (unidentif.)	3	many ♂
							Diptera (unidentified)	1	many ♂
	1	17 Jan. 1979	1:10 P.M.– 2:10 P.M.	cloudy	27– 23.5	1.0			
							Diptera		
							Syrphidae (unidentified)	2	many ♂
							Diptera (unidentified)	1	many ♂
							Hymenoptera		
							Apidae		
							Apis mellifera	1	many ♂
T. tau	3	8 Oct. 1978	3:30 P.M.– 5:30 P.M.	fair to rainy	23.5– 22	2.0	Coleoptera		
							Curculionidae		
							Scaevinus truncatus	1	4 ♂
	3	17 Oct. 1978	3:00 P.M.– 4:20 P.M.	fair	23–22	1.3	*Scaevinus truncatus*	2	1 ♂
	3	18 Oct. 1978	9:30 A.M.– 11:00 A.M.	fair	19.5– 22.5	1.5	Coleoptera		
							Curculionidae		
							Scaevinus truncatus	2	3 ♂
	3	20 Oct. 1978	–	fair	–	spot check	*Scaevinus truncatus*	1	1 ♂
	3	23 Oct. 1978	2:30 P.M.– 3:00 P.M.	fair	25–24	0.5	*Scaevinus truncatus*	2	2 ♂
	3	6 Dec. 1978	–	–	–	spot check	*Scaevinus truncatus*	1	1 ♂
	3	2 Sept. 1979	6:00 A.M.– 11:30 A.M.	fair to rainy	17–23	5.5	*Scaevinus truncatus*	1 (on ♀)	4 ♀, 4 ♂

TABLE 12. **Contents of *Tambourissa sieberi* gynoecious flowers sampled at Mt. Cocotte, Mauritius in January 1979.**

Contents	No. Flowers From Tree	% Total	No. Flowers From Ground	% Total
Empty	10	45.5	15	41.7
Small Coleoptera: (Hydrophilidae, *Dactylosternum vinsoni* B.B.; Nitidulidae, *Carpophilus mutilatus* Er., *Epuraea terminata* Rtt.,[a] *Haptoncus minutus* Rtt., *Lasiodactylus pictus* MacL.; Rhizophagidae, *Europs* cf. *brevis* Gronv.; Staphylinidae, *Atheta dilutipennis* Mots., *Philonthus flavocinctus* Mots.	6	27.3	13	36.1
Lepidoptera (*Opogona sacchari* Bojer, larva, presumably a predator)	1	4.5	5	13.9
Unidentified larvae (possibly Diptera)	2	9.1	0	0
Ants (Hymenoptera, Formicidae)	0	0	1	2.8
Isopod	2	9.1	0	0
Unidentified insect eggs	1	4.5	2	5.5
Total	22	100.0	36	100.0

[a] **Three individuals of *Epuraea terminata* also found on bagged androecious flowers of *T. sieberi* at this site.**

flower contains 80–100 long, dark purple-red setose styles which secrete a slight mucilaginous exudate on the surface (Fig. 16C). Androecious flowers split into 5–7 irregular, flat lobes and contain 100–150 T-shaped stamens with loculi held on lateral arms (Figs. 18H, 39B, C). The pollen is only slightly cohesive. Androecious flower color may be either dark purple-red or greenish white internally. I was unable to detect any floral odor from *T. tau* flowers during either day or night.

A population of *Tambourissa tau* at Perrier Nature Reserve was observed for pollinators for a total of 10.8 hours. The only insect to visit the flowers with any regularity was *Scaevinus truncatus,* a cryptic, nocturnal folivorous weevil found to occur on most species of *Monimia* and *Tambourissa* in Mauritius and Réunion. *Scaevinus* normally feeds on the leaves of *T. tau,* but during the flowering season weevils were found feeding on buds and flowers, grazing on the stamens, styles, and receptacle lobes. Large numbers of pollen grains were found trapped among the insects' body hairs and scales. To test the weevil's vagility, marking experiments were carried out on *Scaevinus* at Perrier. Among 52 individuals of *T. tau* studied, 8–28% were found to harbor *Scaevinus* on a given day. Out of 27 *Scaevinus* marked at the onset of the experiment, 18 (67%) had moved to other plants in the same population after three days. As *T. tau* occurs at comparatively high population densities at Perrier (57 plants/512 m^2, or an estimated 1,113/ha), with nearest neighbor distances averaging only 160 cm (Fig. 3B), and fruit set in the wild is relatively high, it appears that *Scaevinus* is effective in cross pollinating *T. tau.* Although *Scaevinus* was also seen feeding on flower buds of *T. peltata* at Perrier, it was never observed to visit its flowers, nor those of any other *Tambourissa* or *Monimia* species. Finally, no other insects were observed to visit the flowers of *T. tau.*

TAMBOURISSA CORDIFOLIA

A study of this species was carried out at Pétrin Nature Reserve where *Tambourissa cordifolia* is common and forms dense, local populations in a low, scrubby *Philippia* heath formation. It is a small, dioecious shrub 1–2 m high with erect, multiple stems bearing medium-sized solitary or fasciculate flowers on leafless nodes. The androecious flower splits into four flat, spreading-reflexed lobes with 300–400 white stamens (Figs. 20C, 42B), which release white, coalescent pollen. The hollow, obconic gynoecious receptacle is shallow and splits apically into four erect or outcurved deltoid lobes that are ribbed and whitish within (Fig. 42G, H). The floral entrance is 10–12 mm wide and allows access to 100–400 short, purple-red conical styles that produce a sparse surface secretion (Fig. 13E). Flowers of both sexes emit a strong, pleasantly fruity floral odor likened by various observers to that of ripe

TABLE 13. Summary of results of *Tambourissa* crosses carried out in Mauritius (1978–1979) and at the Missouri Botanical Garden (1980).

Species & Locality	No. ♀ Flowers Outcrossed	No. Fruits Developed	% Fruit Set	No. ♀ Flowers Selfed	No. Fruits Developed	% Fruit Set
T. amplifolia, Bel Ombre	8 (3 individuals)	1	12.5	8 (3 individuals)	0	0
T. cordifolia, Pétrin	4 (2 individuals)	3	75.0	(Dioecious)	—	—
T. cordifolia × *T. peltata*,	8 (2 individuals)	1	12.5	—	—	—
T. peltata, Perrier	7 (2 individuals)	7	100.0	(Dioecious)	—	—
T. peltata × *T. cordifolia*	2 (1 individual)	2	100.0	—	—	—
T. purpurea, cultivated, St. Louis	—	—	—	15 (1 individual)	0	0
T. quadrifida, Yemen Valley	15 (3 individuals)	14	93.3	16 (3 individuals)	0	0
T. sieberi, Mt. Cocotte	2 (2 individuals)	2	100.0	11 (2 individuals)	4	36.4
T. sieberi × *T. tau*	2 (1 individual)	2	100.0	—	—	—
T. tau, Perrier	12 (8 individuals)	12	100.0	16 (8 individuals)	0	0

apricots, ripe stewed bananas, or ripe jackfruit, which is perceptible for several meters. The species is dioecious and therefore obligately outcrossing.

A mature flowering individual of each sex was selected for study totalling 23 hours of observation time (Table 11). Pollinator activity began at dawn (ca. 5:45 A.M.) as the dense mists dispersed. Numerous small dipterans then began congregating on both androecious and gynoecious flowers (up to 25 insects per flower; Fig. 20C) drawn by the strong, fruity odor. *Drosophila nasuta* and *Zaprionus vittiger* were the most frequent visitors, with smaller numbers of *Lyciella* and *Homoneura* (both Lauxaniidae) (Table 11). The insects fed on the pollen of the androecious flowers and drank dew and possibly stylar exudate from the gynoecious flowers. Considerable interfloral and interplant movement occurred at this time. Insect activity began to abate after 7:00–8:00 A.M. with an increase in temperature and wind velocity and generally ceased completely by 9:00 or 10:00 A.M.

Pollen grains adhered to the bodies of all the insects examined, suggesting they are effective as pollen vectors, although no actual pollen counts were made. In addition, the population density of *Tambourissa cordifolia* was extremely high at Pétrin (69 individuals/410 m², or an estimated 1,684/ha), with a mean nearest neighbor distance of 78.5 cm (Fig. 3C). Over 50% of the individuals in this population were actually situated within 50 cm of each other (Fig. 3C).

Judging by the relatively high wild fruit set and good regeneration of *Tambourissa cordifolia* at Pétrin, ample cross pollination takes place. As Drosophilidae breed in decaying fruit and fungi, and Lauxaniidae breed in decaying vegetation (Borror & Delong, 1971), it is likely that significant pools of these insects are available during the plants' three to five month flowering period. Significantly, Thien (1980) also recorded two of the same dipteran genera (*Drosophila* and *Homoneura*) as pollinators of *Drimys* in New Guinea.

TAMBOURISSA AMPLIFOLIA

A slender treelet 6–8 m tall, *Tambourissa amplifolia* is occasional to locally common in the understory of some lowland and lower montane wet forest areas in Mauritius. It is monoecious and basally cauliflorous. Flowering takes place from November through January and up to 24 long-pedicellate flowers are open at a given time, each lasting for 10–15 days.

The white androecious flowers split into four flat lobes and resemble those of *Tambourissa cordifolia*, but are only half as large with 150–200 stamens (Fig. 18B). The shallowly napiform gynoecious flowers also resemble those of *T. cordifolia*, but are half as large with four everted lobes, a broad orifice, and ca. 300 short, yellow or purple styles situated in the shallow, discoid receptacle. Only slight amounts of mucilage are secreted by the styles. Flowers of both sexes produce a faint, fruity odor.

One individual of *Tambourissa amplifolia* was observed at Bel Ombre for a total of 4.5 hours during the morning (Table 11). Several drosophilids (*Drosophila* cf. *nasuta* and *Homoneura* sp.) repeatedly visited flowers of both sexes. Al-

TABLE 14. Contents of *Tambourissa quadrifida* gynoecious flowers sampled at Matala Valley (Yemen), Mauritius in March, June, and July 1979.

Contents	No. Flowers From Tree	% Total	No. Flowers Fallen From Ground	% Total
Empty	410	93.6	100	75.8
Mealybugs (Homoptera, probably Pseudoccidae)	1	0.2	15	11.4
Ants (Hymenoptera, Formicidae)	14	3.2	4	3.0
Silk webbing & pupa (probably Lepidoptera)	6	1.4	3	2.3
Silk webbing & larva (probably Lepidoptera)	2	0.5	2	1.5
Coleoptera, Nitidulidae, *Haptoncus luteolus*	1	0.2	—	—
Detritus (feces)	3	0.7	5	3.8
Empty egg cases	1	0.2	2	1.5
Springtail (Collembola)	—	—	1	0.7
Total	438	100.0	132	100.0

though visits were less extensive than in *T. cordifolia,* the same pollinator syndrome appears to be operative. Individuals of *T. amplifolia* are generally separated by distances less than 10 m, which the insects should be able to cross. Outcrossed flowers of *T. amplifolia* yielded a low fruit set (12.5%) although it is unclear why (Table 13).

TAMBOURISSA PELTATA

A medium-sized dioecious canopy tree, *Tambourissa peltata* is common and widespread in wet and cloud forests throughout the island. Flowering lasts from March to June and each individual generally has three to ten flowers open at a given time, although a large androecious plant may produce up to 58 open flowers during peak flowering. The exposed flowers are produced either singly or in groups of two to three on the older, leafless branches in the canopy and on the upper trunk, thus making pollination studies difficult. It is dioecious and obligately outcrossing.

The broad gynoecious receptacle splits open by four or five ornate, dark purple-red verrucose sterile lobes that spread flat, resembling a *Stapelia* flower (Figs. 15A, 17E). The flat gynoecial disc is orange and bears ca. 400–500 flat, densely crowded columnar styles. At anthesis, the entire disc is covered by a layer of thick, sweet mucilage that functions both as a compitum and as nectar. Androecious flowers split gradually into four or five ultimately reflexed lobes bearing 200–400 stamens that release abundant, coalescent pollen (Fig. 17D). Both salmon pink and dark purple-red androecious color morphs occur, according to the individual. Flowers of both sexes produce a strong, sour odor of rotting fruit or tomatoes and persist on the tree for 10–15 days.

The species was studied at Mare Longue Plateau and at Perrier and Pétrin Nature Reserves (Table 11) for a total of 8.2 hours and supplemented by additional insect collections. Most frequent visitors were Diptera, notably Syrphidae and Drosophilidae (Table 11). In the early morning, large numbers of *Drosophila* and *Zaprionus* congregated on both androecious and gynoecious flowers as in *Tambourissa cordifolia,* in addition to a few small Coleoptera (*Enicmosoma, Epuraea*). As the sun rose higher and the temperature increased, the drosophilids gradually left and were replaced by syrphids. The Syrphidae *Askarina* and *Ornida* were active throughout the day, periodically visiting different flowers on the same and on different trees. They often remained on flowers for extended periods to feed on the pollen (up to 43 minutes on a single flower for *Ornida obesa*), and also drank mucilage from the gynoecious flowers. Captured insects were found to have abundant pollen on their bodies. Other insect visitors included honeybees, which visited androecious flowers to gather pollen, but displayed no interest in the gynoecious flowers and their muciliage. The folivorous weevil, *Scaevinus truncatus,* while living on *T. peltata* and feeding on its leaves and young flower buds, did not visit mature flowers and actually displayed an aversion to them, possibly repelled by the strong odor.

At Perrier, *Tambourissa peltata* occurred at comparatively low population densities of 26 individuals/12,700 m^2 (or an estimated 21/ha), with a mean nearest neighbor distance of 975 cm (Fig. 3A). Because of the relatively large distances separating individuals of this dioecious species, the strong-flying syrphids probably represent the most effective pollinators, although the role of drosophilids and small coleopterans as pollinators cannot be dismissed.

TAMBOURISSA FICUS

Tambourissa ficus is related to *T. peltata* but differs in being a small understory tree. It is usually subdioecious, producing one or two open flowers generally of a single sex at the swollen base of the trunk (Fig. 20E, F). Although only five to eight flowers are produced during the flowering season (Sept.–Dec.), they have the greatest dimensions of any in the family.

The urceolate-cupuliform gynoecious flower has a broad orifice and is lined with ca. 1,000–2,000 long, yellowish pink setose styles which secrete small amounts of mucilage (Fig. 15C). Two androecious floral forms occur, the first being cupuliform-urceolate like the gynoecious flower, with erect lobes and white stamens (Fig. 20E). The other form splits open flat into five to seven ultimately reflexed lobes with pinkish purple stamens (Fig. 20F). The thick, apiculate stamens number 900–1,800 in both forms. Flowers of both sexes emit a fetid-aminoid, but slightly fruity, odor.

A tree with flat purple androecious flowers at Brise Fer was observed for 0.8 hours at midday (Table 11). Male and female syrphids of the genus *Eumerus* were attracted to the flowers (Fig. 20F), and both captured insects had pollen adhering to their bodies. The cupuliform white androecious flowers on a tree at Rivière des Galets (Fig. 20E) were visited by a different dipteran (unidentified). At Mt. Cocotte, however, large numbers of small Hydrophilidae beetles of the genus *Cercyon* were found in gynoecious flowers and on open purple androecious flowers on a single tree. Significantly, members of the same family also visited gynoecious flowers of *Tambourissa sieberi* at the same locality, although their role in the pollination of *T. ficus* is uncertain.

Although no crosses were carried out for *Tambourissa ficus,* it is probably at least partly outcrossing because of its tendency towards dioecy. Scattered individuals as well as denser local populations occur, and syrphids would seem to represent the most efficient pollinators, although the Coleoptera may also play a role. More extensive observations on the pollination biology of *T. ficus* are obviously required.

Flowers of *Tambourissa crassa* (Réunion) emit a strong, rancid-fruity odor and appear to display the same pollination syndrome as *T. ficus.* A gynoecious individual of this dioecious species at Col de Bellevue (*Lorence 2468,* MO) was repeatedly visited by an unidentified dipteran which drank the mucilaginous secretion partly filling the mature gynoecious flower (Fig. 20D).

MONIMIA OVALIFOLIA

A low, dioecious tree restricted to small patches of cloud forest on the island's highest mountains, *Monimia ovalifolia* is the only member of the genus to occur in Mauritius. Its numerous small flowers are produced in ramiflorous inflorescences from August to November. The globose gynoecious receptacle takes on a pink to orange color at anthesis, but remains closed except for a small pore through which the six to 12 glistening white styles are exserted (Fig. 14B). These produce a slight surface secretion. The externally yellowish androecious flowers split into four or five recurved valvate segments (Fig. 14A) much like those of *Tambourissa.* The numerous white stamens possess paired basal appendages (as in Fig. 13A) and release coalescent pollen. Flowers of both sexes produce a strong, sweet odor.

Androecious and gynoecious trees of *Monimia ovalifolia* were observed for 2.2 hours at Mt. Cocotte (Table 11). The flowers appear to be myophilous and were repeatedly visited by small, unidentified Syrphidae that licked the styles and fed on the pollen. They were found to carry *Monimia* pollen and could probably traverse the relatively short distances separating individuals of *Monimia* at Mt. Cocotte. It is therefore likely that syrphids are effective pollinators of *Monimia ovalifolia* in Mauritius.

DISCUSSION

Tambourissa species in Mauritius exhibit two different modes of pollination involving Coleoptera and Diptera, modes that occur in a number of other extant primitive angiosperms (e.g., Faegri & van der Pijl, 1971; Gottsberger, 1974; Thien, 1980). Thrips, which are known to visit flowers of other primitive angiosperms including Monimiaceae (Gottsberger, 1977), were not found in this study, although it is possible that they may visit some of the small flowered Comorean and Madagascan species of *Tambourissa.*

Flowers of *Tambourissa quadrifida* and *T. sieberi* seem to be primarily cantharophilous with the fruity odors, dull colors, and numerous floral parts (i.e., stamens and styles) characteristic of this syndrome (e.g., Faegri & van der Pijl, 1971). The inferior ovaries and abundance of receptacular idioblasts (see Morphology and Anatomy section) are probably also protective in this context. Gynoecious flowers of both species are further adapted for pollination by a variety of small, probably allotropic, Coleoptera and differ from the classic Magnoliaceous cantharophilous flower in the following ways: the flowers are long lived, apetalous, and remain permanently open. Furthermore, the gynoecious floral entrance is small, thus excluding many destructive predators, although larvae of the indigenous moth, *Opogona sacchari,* successfully feed on flowers and developing fruits of at least three species, including *T. sieberi* (Table 11). Both species produce only traces of mucilage on their styles and presumably deceive the insects by their strong, ripe fruity odors, although the long styles of *T. sieberi* may also be utilized as food bodies. Androecious flowers of all *Tambourissa* species offer only pollen as a reward, a resource taken advantage of by a variety of Diptera and the introduced *Apis,* as well as by the effective pollinators. Mass flowering of these species may compensate for pollinator inefficiency.

The drab, apparently odorless flowers of *Tambourissa tau* seem to represent a specialized cantharophilous syndrome adapted to pollination by a single insect, the folivorous curculionid, *Scaevinus truncatus,* which feeds specifically on Monimiaceae leaves. The flowers of this species represent a supplementary food source for *Scaevinus,* and *T. tau* has taken advantage of its presence for use as a readily available pollinator. The long styles represent a food source for the insect, while the basal stylar secretions presumably trap pollen grains from its body and legs. The peculiar T-shaped stamens with widely separated loculi may maximize pollen contact with *Scaevinus,* while also rendering the pollen load less liable to be eaten at once. In any case, flowers of *T. tau* differ from the usual cantharophilous flowers and appear to be highly specialized. The energetic aspects of this relationship (cf. Heinrich & Raven, 1972) should prove to be most interesting.

The predominantly myophilous flowers of *Tambourissa amplifolia, T. cordifolia, T. ficus,* and *T. peltata* share a number of cantharophilous features with those of *T. quadrifida* and *T. sieberi,* i.e., strong fruity or aminoid odors and drab colors (in *T. ficus* and *T. peltata*). In fact, the latter two species also attracted some Coleoptera (Table 11), which is perhaps suggestive of a shift from cantharophily to myophily in *Tambourissa.* A number of other trends in these species suggest adaptations to allotropic fly pollinators (cf. Faegri & van der Pijl, 1971), including: paler floral colors (white androecious and pale yellow or pink gynoecious flowers in *T. cordifolia* and *T. amplifolia,* with white and salmon pink morphs occurring in androecious flowers of *T. ficus* and *T. peltata,* respectively), apically confluent anther loculi presenting the pollen more effectively (*T. amplifolia, T. cordifolia, T. peltata*); shallower and broader gynoecious receptacles with a larger entrance (extreme in the flat, discoid flowers of *T. peltata*), surrounded by attractive, spreading sterile lobes that act as landing platforms; more copious, sweet mucilaginous exudate with a nectar function in the gynoecious flower (*T. peltata,* Figs. 15A, 17E); a shortening of the stamens and styles to accommodate the insects' short probosces.

Although certain common features occur in these species, there appear to be two distinct trends. The first is a "fruit fly" syndrome involving small drosophilids that occurs in *Tambourissa amplifolia* and *T. cordifolia.* These plants are small in stature, occur in comparatively dense populations, and have smaller and paler flowers with a sweet, fruity odor produced near the ground. Significantly, Thien (1980) recorded two of the same fly genera as pollinators of *Drimys* in New Guinea, suggesting that these insects may pollinate a greater number of extant primitive angiosperms than previously suspected.

The second trend involves larger and more vigorous flies, primarily syrphids (in *Tambourissa ficus* and *T. peltata*). These are larger, more widely dispersed forest trees with more massive, pinkish to purplish flowers that emit sour, rancid, or otherwise fetid-aminoid odors with fruity overtones. Flowers are produced on the leafless upper branches (*T. peltata*) or near the ground

(*T. ficus*) and are exposed for easy access by the insects. Although androecious flowers of *T. ficus* were visited by syrphids and another dipteran in two cases (Table 11), flowers of both sexes of another individual attracted numerous hydrophilid beetles (*Cercyon* sp.). Hydrophilids were also found in gynoecious flowers of *T. sieberi* at this same site. A more thorough study of *T. ficus* is needed to detail its significant pollinators.

Monimia ovalifolia displays a number of myophilous features, namely, a sweet floral odor, yellow to pink or orange receptacles, shallow, permanently open white androecious flowers, well exposed stamens and styles. Its flowers are well adapted to the small, probably allotropic syrphids that visit them.

In summary, species of *Tambourissa* in Mauritius exhibit two different modes of pollination based on Coleoptera and Diptera, and each mode displays two distinct trends involving modifications in size, shape, color, and odor of the flower. Pollinator modes also appear to be related to demography and life forms. Pollinator specialization presumably contributes to reproductive isolation in simultaneously flowering sympatric species (e.g., *Tambourissa amplifolia* and *T. tau*). Another factor contributing to reproductive isolation between sympatric species is different flowering times, clearly operative in *Monimia* species in Réunion (see section on Habitat and Ecology), and also for Mauritian *Tambourissa* species with common pollinators (e.g., *T. ficus* flowers from September to December; *T. peltata* flowers from March to June). Reproductive isolation appears to be effective, as hybridization is extremely rare in the wild in Mauritius, although artificial crosses resulted in fruit set in three different interspecific combinations (Table 13).

Prolonged flowering periods and high floral output may compensate for low pollinator efficiency. Finally, dioecism and self-sterility in monoecious species can be viewed as representing mechanisms to enforce outcrossing (e.g., Bawa, 1974; Bawa & Opler, 1975). Self-compatibility in *Tambourissa sieberi* most likely offsets low population densities and low efficiency of its small pollinators.

SYSTEMATIC TREATMENT

MONIMIACEAE Jussieu, Ann. Mus. Natl. Hist. Nat. 14: 133. 1809 (sub Monimiées).

Evergreen trees or shrubs, rarely lianas, usually aromatic, frequently dioecious or monoecious, sometimes hermaphroditic. Leaves simple, usually opposite and decussate, rarely ternate, alternate or anisophyllous, exstipulate, with laminar oil glands, the trichomes simple, fasciculate and/or stellate, the venation festooned brochidodromous, rarely craspedodromous, the margin entire or serrate to dentate with glandular teeth. Inflorescence cymose or thyrsic, or the flowers fasciculate or solitary, either terminal, axillary, ramiflorous or cauliflorous, the bracteoles small and caducous; flowers small to large, actinomorphic, rarely oblique, bisexual, polygamous or unisexual, the receptacle ± well developed, globose, ovoid to obovoid, urceolate, napiform, campanulate or discoid, the tepals subequal, spiral, whorled or decussate, large and petaloid to small or ± lacking; androecious flowers with few to numerous stamens in 1–many series or irregularly disposed, the filaments usually short and flattened, occasionally with a pair of basal appendages, the anthers erect, (2–)4-sporangiate, the loculi separate or confluent apically or rarely basally, lateral or ± unifacial, valvate or longitudinally dehiscent; gynoecious flowers with or without staminodes, the carpels several to numerous, rarely solitary, unilocular, shortly stalked or sessile, free or enclosed or immersed in the receptacle wall, the style short or elongated, the stigma terminal, dry or secreting mucilage, the ovule solitary, erect, horizontal or pendulous. Fruiting carpels exposed, or enclosed or immersed in the accrescent receptacle wall, indehiscent, often drupaceous with a membranous or fleshy mesocarp and/or aril-like appendage, or plumose (Atherospermoideae); endocarp membranous to bony, the seed erect to pendulous, the testa membranous, the endosperm abundant, oily and fleshy, the embryo straight, the cotyledons erect or divaricate.

The Monimiaceae sensu lato include the subfamilies Atherospermoideae, Hortonioideae, Siparunoideae, Monimioideae, and Mollinedioideae, and comprise some 30 genera and nearly 350 species in the tropics and subtropics, with the greatest diversity occurring in the southern hemisphere.

KEY TO GENERA OF MONIMIACEAE IN THE MALAGASY REGION

1a. Trichomes of leaf and stem in part or all stellate with 4–16 horizontal rays, the others simple or in fascicles of 2–4; abaxial laminar surface obscured by a dense, whitish indument of trichomes; stamens bearing a pair of appendages on filament (Monimioideae) .... 1. *Monimia*

1b. Trichomes of leaf and stem either simple or rarely in fascicles of 2–4, never stellate; abaxial laminar surface visible, not obscured by trichomes; stamens lacking appendages on filament (Mollinedioideae).
  2a. Gynoecious receptacle flat and discoid to ± concave, the carpels superior, subsessile to sessile, free on the disc, clavate to columnar; fruiting receptacle ± discoid, concave to convex, bearing the exposed, ± free drupes, not splitting at maturity.
    3a. Buds and flowers with 7–15 large, thick obtuse tepals imbricate in 1–2 radial series; male floral receptacle unfolding gradually at anthesis, not splitting .... 2. *Decarydendron*
    3b. Buds and flowers with 4–8(–16) small to minute decussate tepals; male floral receptacle splitting into 4 valvate segments at anthesis ...... 3. *Ephippiandra*
  2b. Gynoecious receptacle ± urceolate, cupuliform to napiform, ellipsoid or cylindric (discoid in *T. peltata*), the carpels inferior, syncarpous, immersed in the receptacle wall; fruiting receptacle ± closed, the drupes immersed in the wall, splitting open irregularly at maturity .... 4. *Tambourissa*

Monimia Thouars, Hist. Vég. Iles France 35, tab. 9. 1804; Thouars, Hist. Vég. Iles Austral. Afriq. ed. 1: 35, tab. 9. 1805; Willd., Sp. Pl. 4(2): 647. 1805; Juss., Ann. Mus. Natl. Hist. Nat. 14: 116. 1809; Poir., Encycl. Suppl. 3: 726. 1813; Spreng., Syst. 3: 906. 1826; Boj., Hortus Maurit. 289. 1837; Tul., Monogr. Monim. 307. 1855; A.DC., Prodr. 16(2): 661. 1868; Baill., Adansonia, Ser. 1, 9: 133. 1868–1870; Baill., Hist. Pl. ed. 2, 1: 299. 1871; Benth. & Hook., Gen. Pl. 3: 139. 1883; Baker, Fl. Mauritius 289. 1877; Hobein, Bot. Jahrb. Syst. 10: 56. 1889; Pax, Pflanzenfam. 3(2): 101. 1891; Cordem., Fl. Réunion 299. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 65. 1901; Perk, Pflanzenr. 4, 101 (Nachtr.): 39. 1911; Vaughan, Mauritius Inst. Bull. 1: 76. 1937; Hutch., Gen. Fl. Pl. 1: 118. 1964. LECTOTYPE: *M. rotundifolia* Thouars, cf. Bullock, Kew Bull. 14: 44. 1960.

Dioecious pubescent aromatic evergreen trees, rarely shrubby; bud scales present. Leaves opposite, decussate, entire, strongly discolorous, the abaxial surface obscured by a dense indument of simple, fasciculate and/or stellate-peltate trichomes, the venation festooned brochidodromous. Inflorescence pubescent, a thyrse or cyme, rarely leafy, either ramiflorous, axillary or subfoliar on leafless nodes, rarely terminal, the bracts and bracteoles caducous, the flowers borne in umbelloid units of 2–7. Male receptacle pedicellate, obovoid or globose in bud, the apex with several pairs of minute, decussate tepals, splitting at anthesis into 4–6 ± regular valvate segments, tomentose within, the short stamens numerous, multiseriate, the filament thin, subtended by a pair of basal appendages, the connective and filament reddish brown, full of oil cells, blunt or slightly prolonged and rounded, the anther ovoid, bilocular, the loculi separate, parallel, longitudinally dehiscent, introrse; pollen inaperturate, spheroid, spinose. Female receptacle pedicellate, globose-urceolate to ovoid-urceolate, the apex with several pairs of minute decussate tepals, the carpels 4–14 per flower, unilocular, subsessile, free, enclosed within the receptacle which is lined with dense, simple hairs, the styles simple, ± papillose, exserted through the narrow, 3–5-lobed orifice at anthesis, the ovule solitary, pendulous, anatropous. Ripe fruiting receptacle splitting into 3–5 irregular valvate lobes, pinkish red and partly velutinous within, exposing 4–12 ovoid-compressed fruiting carpels (drupes) surrounded by a fleshy orange mesocarp, the apical half covered by a fleshy orange stylar aril, the endocarp whitish, thick, bony, mucronate, and longitudinally crested, the surface foveate, foveate-reticulate to foveate-sulcate.

Distribution. *Monimia* consists of three species endemic to the Mascarene Islands of Mauritius and Réunion. The presence of *Monimia* in Rodrigues is doubtful and based on a single collection of *M. ovalifolia* (*Balfour s.n.*, K). As Balfour failed to mention the genus in his comprehensive work on the botany of Rodrigues (1879), I suspect the specimen is wrongly labelled and may actually have come from Réunion where Balfour also collected. The *Balfour s.n.* collection most closely resembles plants of *M. ovalifolia* from Réunion characterized by orbiculate leaves. Furthermore, Rodrigues does not even attain the minimum altitude at which the species occurs in Mauritius and Réunion.

TAXONOMIC HISTORY OF *MONIMIA*

Monimia was described by A. Du Petit-Thouars in 1804 based on two species, *M. ovalifolia* and *M. rotundifolia*, which he collected in Mauritius and Réunion respectively. Du Petit-Thouars described the genus accurately and noted the close similarity between the androecious flowers of *Monimia* and those of *Tambourissa* (as *Ambora* Juss., and *Mithridatea* Comm. ex Schreb.). As *Monimia* differed from the latter most conspicuously in the structure of its gynoecious flowers, he named it after Monima, wife of Mithridates.

In 1809, Jussieu created a new family (as Monimieae) for *Monimia, Tambourissa* (as *Ambora*), and four other genera of Monimiaceae, which were all previously placed in the Urticaceae by various authors. Willdenow (1805) and Sprengel (1826) placed *Monimia* in subgroups of their "Dioecia," along with other anomalous genera belonging to unrelated families, but followed Du Petit-Thouars in noting its affinities to *Tambourissa.*

In his monograph of the family, Tulasne (1855b) placed *Tambourissa* and *Monimia* in separate tribes. *Monimia* was included in his "Drupaceae" (Monimieae) together with *Siparuna* Aubl. (as *Citrosma* Ruiz & Pav.), *Mollinedia* Ruiz & Pav., *Kibara* Endl., *Hedycarya* Forst., and *Peumus* Mol. (as *Boldea* Juss.) on the basis of their free, drupaceous carpels. Tulasne (1855b) also described an additional species of *Monimia, M. citrina,* which I consider to be synonymous with *M. rotundifolia.* Baillon (1868–1870, 1871) generally followed Tulasne, including *Monimia* under his "*Hortonia* series" (Hortonieae) with many of the same genera as Tulasne, although he included a number of others also having free, drupaceous carpels.

Bentham and Hooker (1883) recognized two large tribes of Monimiaceae on the basis of staminal dehiscence and position of the ovule. They placed *Monimia* with the bulk of genera now included in the Monimiaceae sensu stricto, a treatment largely followed by Hutchinson (1964).

Monimia has been placed in the tribe Monimieae within the subfamily Monimioideae, along with *Tambourissa, Palmeria* F. Muell., and *Hennecartia* Poisson by Pax (1891), Perkins and Gilg (1901), and Perkins (1911). Schodde (1970) created a separate subfamily for *Peumus* based on features of wood, pollen, and chromosome number but ignored *Monimia,* leaving it in the Monimioideae with the bulk of Monimiaceae sensu stricto. More recently, Thorne (1974) joined *Monimia* with *Peumus* as the sole members of the subfamily Monimioideae and created a new subfamily, the Mollinedioideae, to house the remaining genera formerly included in the Monimioideae.

SYSTEMATIC POSITION OF *MONIMIA*

Baillon (1871), Money et al. (1950), and Cavaco (1965) all noted floral morphological similarities between *Monimia* and *Palmeria.* In addition, the wood of *M. ovalifolia* and several species of *Palmeria* shows similar advanced trends (Garratt, 1934; Money et al., 1950). Other shared characters in *Monimia* and *Palmeria* include a dense indument of simple, fasciculate and stellate trichomes, an urceolate gynoecious receptacle enclosing a small number of subsessile or sessile carpels, and a fruiting receptacle which splits open to reveal the ripe carpels set against a pink or red inner surface (Corner, 1976; Endress, 1980b). In spite of superficial similarities in the fruiting receptacles of the two genera, however, which may represent parallel lines of evolution, important differences also exist. The carpels of *Palmeria* are anatomically different from those of *Monimia* and possess a well-developed, hard and shiny black exocarp and thin mesocarp of starch-filled cells absent in the latter (Corner, 1976).

Monimia appears to have closer affinities with *Peumus,* a monotypic genus endemic to Chile. Both genera have horizontal axillary buds, stamens with paired appendages on the filaments, large, spinose pollen grains, the spines and surface composed of cable-like strands (smaller and spinulose in *Palmeria*), receptacles covered by a dense indument of simple, fasciculate and stellate trichomes, carpels with a fleshy mesocarp surrounding the bony white, sculptured endocarp (Fig. 19A, B), and also share the dioecious habit.

In *Peumus,* however, the stamens are tetrasporangiate and dehisce laterally, whereas in *Monimia* they are bisporangiate and dehiscence is nearly introrse along the inner margin (Fig. 13A). In these respects *Monimia* and *Peumus* appear to provide a link between the Atherospermoideae, with their bisporangiate anthers having valvate dehiscence and similar staminal appendages, and the Mollinedioideae, which have tetrasporangiate anthers with lateral dehiscence and lack staminal appendages (Sampson, 1969a, 1969b). As a result, the two genera do not fit satisfactorily into either subfamily.

Specialization in Monimiaceae is generally considered to be expressed in terms of floral simplification and reduction, both in terms of size and number of parts (Money et al., 1950; Endress, 1980b). In these respects, *Monimia* has attained a greater degree of floral morphological specialization than *Peumus,* in spite of the latter's more specialized wood anatomy (Garratt, 1934; Money et al., 1950; Lemesle & Prichard, 1954). Although also dioecious, *Peumus* has retained a greater constellation of unspecialized floral characters, i.e., an elaborate perianth of whorled petaloid and sepaloid tepals, and a broad, shallow floral receptacle bearing exposed carpels in the manner of the putatively primitive *Hortonia* (Lemesle & Prichard, 1954; Endress, 1980a). Flowers of *Monimia* have reduced, scale-like decussate tepals, are closed in bud, and the female receptacle encloses the carpels—all advanced features.

Similarities which *Monimia* shares with *Peumus,* and to a lesser degree with *Palmeria,* suggest possible origin from a common ancestral stock. A *Monimia* precursor may have originally existed in Africa or Madagascar where it subsequently became extinct, but not before reaching the Mascarene Islands via long distance dispersal. The Mascarenes thus provided a refuge for *Monimia.*

Current work with sieve tube plastid analysis by Behnke (1977, and pers. comm.) has shown that *Palmeria* and *Peumus* possess fundamentally different types of sieve tube plastids (S-type and P-type, respectively). As *Monimia ovalifolia* possesses S-type plastids (Behnke, pers. comm.), this feature at least would seem to deny a close relationship to *Peumus.* Sieve element plastids unquestionably provide an additional taxonomically useful character when used in conjunction with other available data, but do not provide an adequate basis for fragmenting the Monimiaceae into some five families as proposed by Behnke (1981).

In summary, *Monimia* displays a number of advanced features, certain of which (i.e., its stamens) are transitional between the Mollinedioideae and the Atherospermoideae. As *Monimia* shares the greatest constellation of features with *Peumus,* however, the two genera are best placed together as constituting the Monimioideae as proposed by Thorne (1974).

KEY TO THE SPECIES OF *MONIMIA*

1a. Leaves amplexicaul with a deeply cordate base, sessile to subsessile; Réunion .... 1. *M. amplexicaulis*
1b. Leaves distinctly petiolate, the base neither deeply cordate nor amplexicaul; Réunion and Mauritius.
    2a. Stems, petioles and inflorescence hirsute-velutinous; trichomes on adaxial surface of lamina mixed simple, fasciculate and stellate with free, ± ascending arms; Réunion .... 2. *M. rotundifolia*
    2b. Stems, petioles and inflorescence at most scabrous or scurfy, not velutinous; trichomes on adaxial surface of lamina uniformly stellate-peltate with horizontal arms united basally for ⅓–½ their length; Réunion and Mauritius .... 3. *M. ovalifolia*

1. Monimia amplexicaulis Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 294, pl. 1, fig. 1a. 1982. TYPE: Réunion. Hauts du Tévelave: forestry road along the Domanial line, cloud forest transitional to heath formation, ca. 1,700 m, 6 Mar. 1979 (fl, fr), *Lorence 2504* (holotype, MO; isotypes, K, MAU, P, REU, Z).

Shrub or small tree attaining 10 m tall and 30 cm diam., the bark grayish brown, longitudinally fissured, the new growth pale grayish to fulvous, velutinous-tomentose with predominantly short-armed stellate trichomes, mixed with long simple and fasciculate trichomes 0.5–1 mm long, the mature leafy stems 3–5 mm diam., velutinous-tomentose. Leaves opposite, sessile to subsessile; petiole stout, 3–5 mm long by 3–5 mm diam., velutinous-tomentose; lamina subcoriaceous to coriaceous, ovate to broadly ovate, broadly elliptic to suborbiculate, (40–)60–130 mm by (32–)40–110 mm, the apex shortly acute, shortly acuminate, mucronate or rounded, the base deeply cordate, amplexicaul, the secondary veins (4–)5–7 pairs, making a 40–60° angle with the costa, the venation depressed adaxially, visible to 3°, prominent and raised abaxially, visible to 4°, the adaxial laminar surface pubescent with predominantly stellate trichomes with 4–12 short horizontal arms, mixed with varying proportions of long simple and fasciculate trichomes with 2–4 ascendant arms, eventually glabrescent and ± pustular, glandular, the abaxial surface obscured by a dense whitish to pale yellowish indument of the same trichomes, the margin entire, pubescent, plane to slightly revolute. Inflorescence a congested, fulvous velutinous-tomentose thyrse or rarely short cyme of (3–)7–37 flowers (gynoecious inflorescence more congested than the androecious), branching to 2°(–3°), leafy or not, ramiflorous or subfoliar on leafless nodes (the primary axis often continuing to grow as a leafy stem), axillary or rarely terminal, the floral axis (5–)10–60(–75) mm by 2–3 mm, often subtended by 1–several pairs of caducous, brown ciliate-pubescent naviculate bracts to 7 mm by 3 mm, the peduncle 4–12 mm long, bearing an umbelloid unit of (2–)3(–6) flowers, occasionally subtended by a caducous, velutinous bracteole to 2 mm long or by a small leaf. Androecious flower in bud ellipsoid to obovoid, 2–7 mm long by 3–5.5 mm diam., velutinous-tomentose, the pedicel 3–7 mm by 1–1.5 mm, often subtended by 1–2 minute subulate bracteoles; at anthesis deeply 3–6-fid, 10–13 mm diam., the lobes ultimately reflexing; stamens (40–)60–150, 1.5–2.5 mm long, the anthers ellipsoid, ca. 1 mm wide, occupying ca. ⅓–½ total length of the stamen, the connective slightly prolonged and rounded, the internal receptacle surface tomentose, the simple hairs 0.3–0.8 mm long. Gynoecious flower in bud globose-urceolate to ovoid-urceolate, 4–5 mm long by 3–4 mm diam., at anthesis the orifice 0.8–1.2 mm diam., the styles 5–10, exserted for 1–2 mm, the internal receptacle surface velutinous with simple hairs 0.5–1.5 mm long, the pedicel 1.5–2.5 mm by 1–1.5 mm. Fruiting receptacles in clusters of 1–10 on the leafless branches, ovoid to subglobose, 7–15 mm diam., externally pubescent with stellate, fasciculate and simple trichomes, the carpels 1–10 per receptacle, ovoid to ellipsoid, 5–7 mm long by 3–5 mm thick, mucronate, with a longitudinal crest, the endocarp deeply foveate-reticulate. Figure 21.

Distribution. Endemic to Réunion (Fig. 22).

Habitat. Monimia amplexicaulis is occasional to abundant locally as a component of mid to upper level cloud forest and lower limits of the *Philippia* heath formations from ca. 1,400 to 2,100 m. It is most frequent on the sheltered, leeward escarpments of the "cirques," e.g., at Petit Matarum, Coteau Kerveguen above Cilaos, Hauts du Tévelave, etc.

RÉUNION. CIRQUE DE CILAOS: ascent to Col de Taibit, 22 Mar. 1974 (fr), *Bosser 21677* (P); Plaine des Fraises, below Col de Taibit, 1,900 m, 2 Feb. 1967 (fl), *Cadet 663 bis* (REU); Cilaos to Col de Taibit, 1,950 m, 22 Mar. 1974 (fr), *Coode 2558B* (K); Montée Cilaos, Coteau Kerveguen, Feb. 1971 (fl, fr), *Bosser 20752* (P); path to Coteau Kerveguen, 1,500 m, 16 Nov. 1973 (fr), *Cadet 4512* (REU); Coteau Kerveguen, 1,500–1,700 m, 24 Feb. 1979 (fl), *Lorence & Rolland 2443* (MAU, MO); (fl), *Lorence & Rolland 2444* (MAU, MO); forest of Mare à Joseph, 1,400 m, 10 Jan. 1967 (fl), *Cadet 663* (REU); 1,200–2,000 m, Aug. 1943 (fl), *Rivals s.n.* (TL-R); 2,000 m, 11 June 1943 (fr), *Rivals s.n.* (TL-R); wet forest at Petit Matarum, 2,000 m, 22 Feb. 1975 (fl, fr), *Cadet 5049* (REU); (fl), *Cadet 5050* (REU); 4 Feb. 1968 (fl), *Capuron 28210-SF* (P); 6 Mar. 1971 (fl), *Friedmann 1118* (P); (fr), *Friedmann 1119* (P); path to Piton des Neiges, 15 Apr. 1978 (fl, fr), *Bosser 22498* (P); 28 Mar. 1973 (fr), *Lorence sub MAU 15693* (MAU); (fl, fr), *Rivals s.n.* (TL-R). CIRQUE DE MAFATE: Col de Fourche, 1,800 m, 29 May 1976 (fr), *Cadet 5435* (REU); valley of Bras Bémale, 1,500 m, 13 May 1976 (st), *Cadet 5404* (REU); above Belier, on Sentier des Scouts to Aurère, 1,500 m, 14 May 1976 (st), *Richardson 4132* (K). PLAINE DES CAFRES: base of Piton Bleu, 1,500 m, 11 July 1943 (fl), *Rivals s.n.* (TL-R); (fr), *Rivals s.n.* (TL-R); 24 Feb. 1945 (fr), *Rivals s.n.* (TL-R); path to Coteau Maigre, 2,100 m, Feb. 1971 (fl), *Bosser 20475* (P). PLAINE DES CHICOTS: 1,900 m, 19 Feb. 1945 (fr), *Rivals s.n.* (TL-R). PLAINE DES MERLES: Cirque de Salazie near La Nouvelle (sic), 1,300 m, 17 Feb. 1944 (fl), *Rivals s.n.* (TL-R). PLAINE DES SALAZES: Sources Bras Cabot, 17 Aug. 1944 (st), *Rivals s.n.* (TL-R). PLAINE DES TAMARINS: 20 Aug. 1944 (st), *Rivals s.n.* (TL-R). HAUTS DU TÉVELAVE: 1,700 m, 21 Sept. 1974 (fr), *Cadet 4797* (REU); (fl), *Cadet 4797 bis* (REU); along the Domanial line, 1,700 m, 6 Mar. 1979 (st), *Lorence 2501* (MO); (fl), *Lorence 2502* (MAU, MO); (fl, fr), *Lorence 2503* (MAU, MO).

Monimia amplexicaulis shares morphological features with *M. rotundifolia,* including the presence of three types of foliar trichomes (stellate, fasciculate, and simple; Fig. 9A). In *M. amplexicaulis,* the trichomes are predominantly stellate with short arms and not predominantly long, fasciculate and simple as in *M. rotundifolia. Monimia amplexicaulis* further differs from the latter by its sessile, deeply cordate, and amplexicaul leaves with 5–7 secondary veins and generally occurs at somewhat higher elevations in more sheltered habitats than *M. rotundifolia,* often at the cloud forest/heath formation interface.

Vernacular names. Mapou, Mapou des hauts (Réunion).

2. **Monimia rotundifolia** Thouars, Hist. Vég. Iles France 35, tab. 9, fig. 2. 1804; Thouars, Hist. Vég. Iles Austral. Afriq. 21, 34, tab. 7, fig. 2. 1805; Willd., Sp. Pl. 4(2): 647. 1805; Spreng., Syst. 3: 906. 1826; Poir., Encycl., Suppl. 3: 727. 1843; Tul., Ann. Sci. Nat. (Paris) 4(3): 32. 1855; Tul., Monogr. Monim. 310, tab. 29a–j. 1855; A.DC., Prodr. 16(2): 661. 1868; Cordem., Fl. Réunion 299. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 66, fig. 18A–D. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 39. 1911 (excluding *Balfour s.n.* collection from Rodrigues); Perk., Gatt. Monim. fig. 34A–D. 1925. TYPE: Ile Bourbon (Réunion). Without precise locality (ca. 1800–1801), *Petit-Thouars s.n.* (holotype, P).

Ambora tomentosa Bory, Voy. Iles Afrique 1: 317, tab. 13. 1804. *Myrtus villosa* Spreng., Syst. 2: 487.

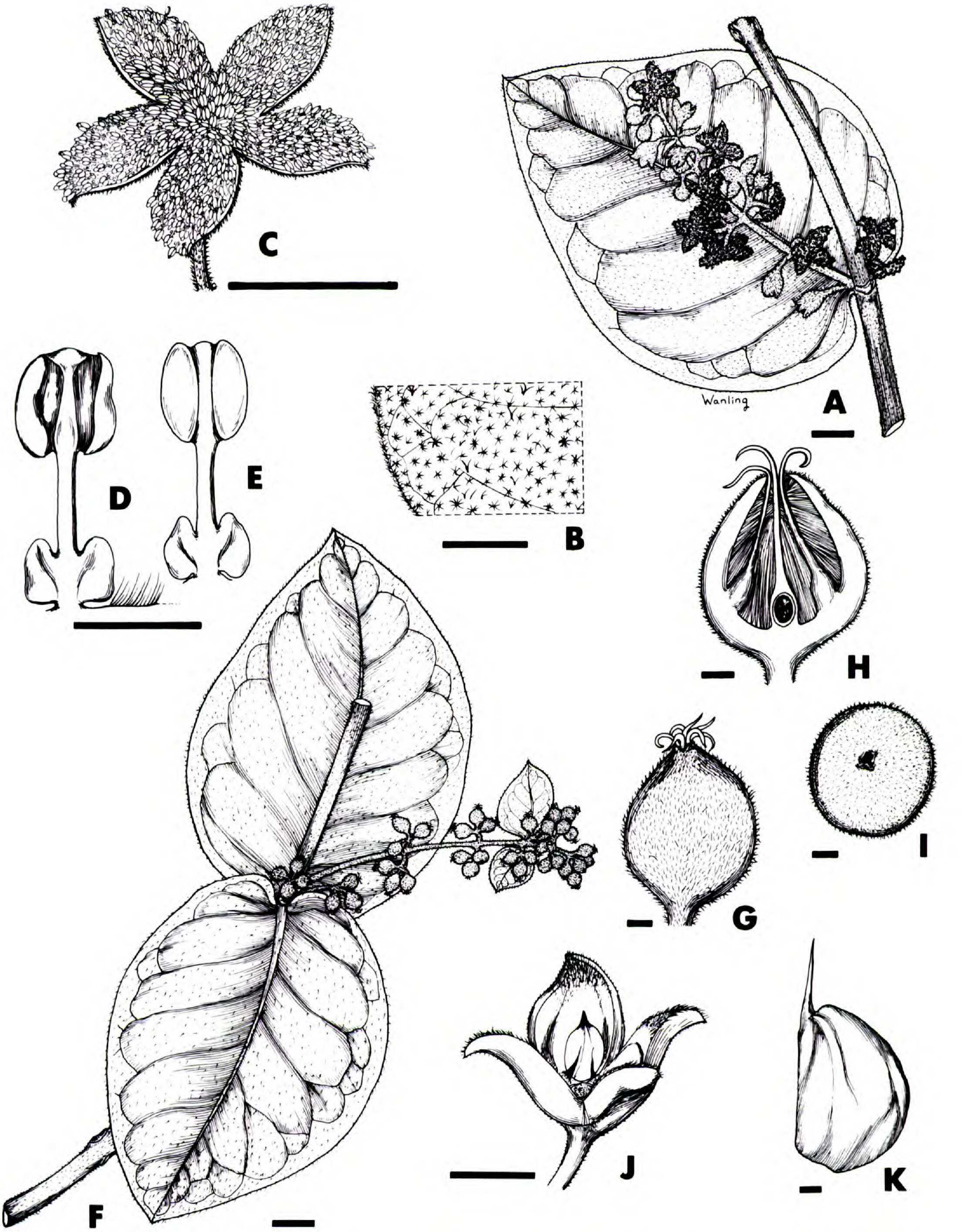

FIGURE 21. *Monimia amplexicaulis* Lorence.—A. Habit, male, one leaf removed.—B. Detail of adaxial leaf surface.—C. Androecious flower at anthesis.—D. Stamen, adaxial view.—E. Stamen, abaxial view.—F. Habit, female.—G. Gynoecious flower at anthesis, lateral view.—H. Gynoecious flower at anthesis, longitudinal section.—I. Gynoecious flower, apical view to show pore (styles removed).—J. Ripe fruiting receptacle, dehisced.—K. Fruiting carpel, lateral view. A–E. *Lorence 2444* (MO). F, J, K, *Lorence 2404* (MO). G–I. *Lorence 2503* (MO). Bars equal 10 mm in A–C, F, J, and 1 mm in D, E, G–I, K.

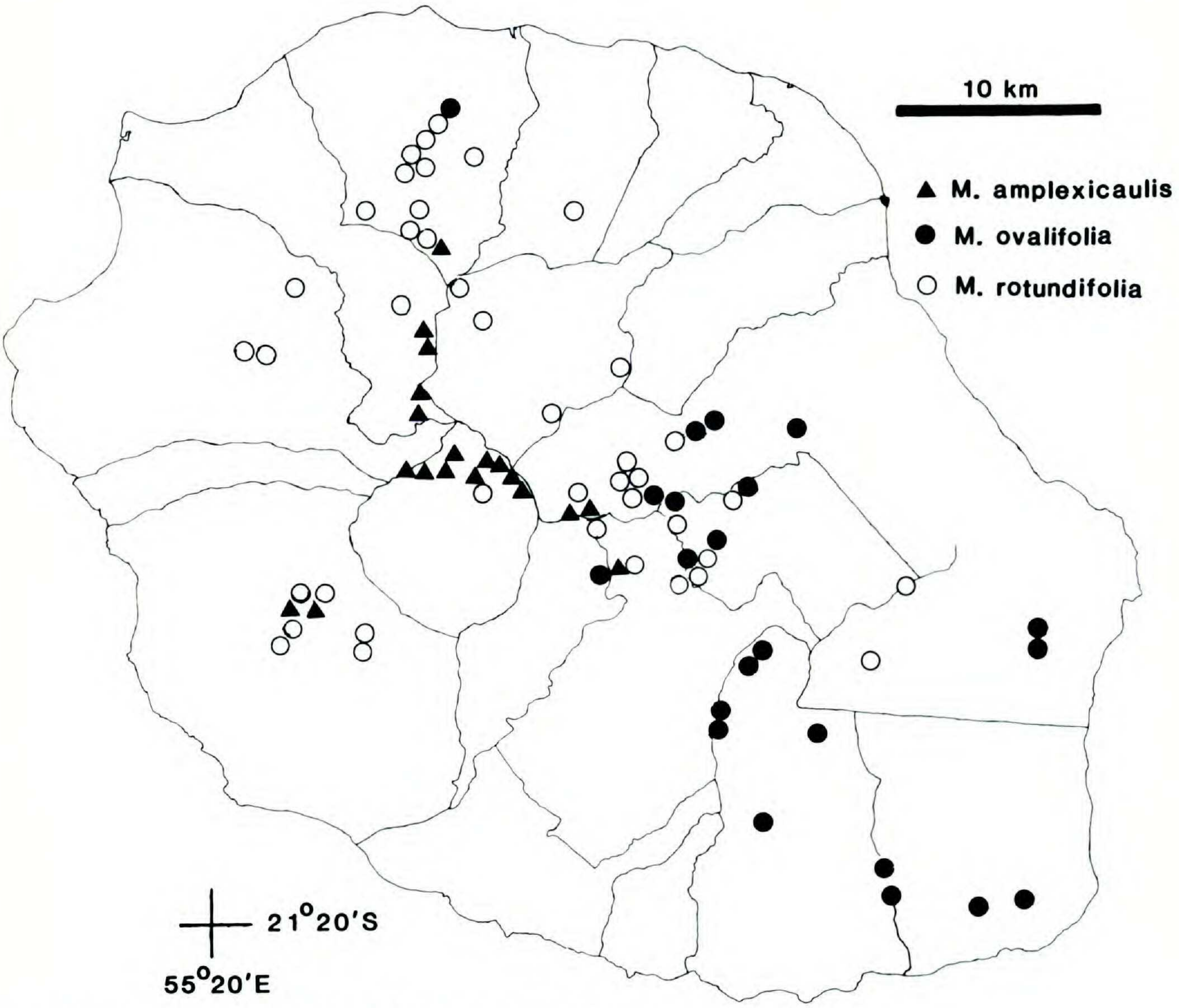

FIGURE 22. Distribution map of *Monimia* in Réunion.

1825, nom. superfl., based on type of *Ambora tomentosa* Bory. *Eugenia villosa* (Spreng.) Poir., Encycl., Suppl. 3: 124. 1843, nom. superfl. TYPE: without precise locality (probably Réunion), *Bory de St. Vincent s.n. in 1821* (holotype, G-DC, n.v.; microfiche, MO).

Monimia citrina Tul., Ann. Sci. Nat. (Paris) 4(3): 32. 1855; Tul., Monogr. Monim. 311. 1855; A.DC., Prodr. 16(2): 661. 1868; Perk. & Gilg, Pflanzenr. 4, 101: 65. 1901. TYPE: Ile de Bourbon (Réunion): without precise locality, *Gaudichaud s.n. in 1836–1837* (lectotype, P, here designated; isolectotype, P).

M. ovalifolia sensu Cordem., Fl. Réunion 300. 1895 non Thouars.

Shrub or low tree attaining 10 m tall and 60 cm diam., the new growth velutinous-tomentose, pale gray to fulvous, the simple and fasciculate trichomes 0.5–1 mm long, mixed with short stellate trichomes, the mature leafy stems 3–6 mm diam., velutinous-tomentose. Leaves petiolate; petioles 5–20 mm by 2–4 mm, velutinous-tomentose; lamina coriaceous, ovate to broadly ovate, elliptic to broadly elliptic or orbiculate, (35–)45–150 mm by (23–)35–160 mm (attaining 320 mm by 300 mm on vigorous sucker shoots), the apex shortly acuminate, acute, mucronate, obtuse, rounded or rarely retuse, the base acutely decurrent, acutely cuneate, obtuse, rounded or shallowly cordate, the secondary veins 3–7 pairs, making a 45–60° angle with the costa, the venation depressed adaxially, visible to 3°, abaxially raised and visible to 4°, the adaxial laminar surface strigose-hirsute, generally with predominantly long, simple hairs and fasciculate trichomes with 2–4 long, ascendant arms, mixed with varying proportions of stellate trichomes with 4–12 shorter horizontal arms, the surface glandular, eventually ± pustular, the abaxial laminar surface obscured by a dense, whitish to pale yellowish indument of the same trichomes, the margin entire, pubescent, plane to slightly revolute. Inflorescence a congested to lax thyrse (rarely a short cyme) of (3–)6–76 flowers (the gynoecious inflorescence more congested than the androecious), branching to 2–3°, leafy or not, velutinous-tomentose, either ramiflorous, subfoliar on leafless nodes (the primary axis sometimes continuing to grow as a leafy shoot), or axillary, the floral axis (7–)15–90(–130) mm by 1.5–2.5 mm, often subtended by 1–4 pairs of brown, scale-like, pubescent or ciliate bracts to 10 mm by 4 mm, the secondary axes 2–25(–50) mm long, occasionally subtended by a single caducous brown bracteole 2–3 mm long, the peduncle 2–12 mm long, bearing an umbelloid unit of 2–6 flowers. Androecious flower in bud ellipsoid, obovoid or subglobose, 4.5–8 mm by 3–5 mm, velutinous-tomentose, the pedicel 3–13 mm by 0.5–1 mm, often subtended by 1–2 minute bracteoles; at anthesis deeply 3–5-fid, 4–14 mm diam., the lobes ultimately reflexing; stamens (25–)50–105, 2–3.5 mm long, the anther 1–1.4 mm wide, ellipsoid, occupying ¼–½ total length of the stamen, the connective ± thickened, blunt or slightly apiculate, the internal receptacle surface tomentose, the hairs simple. Gynoecious flower in bud ovoid-urceolate to globose-urceolate, 3.5–5 mm by 2.5–4 mm; at anthesis the orifice 1–1.2 mm diam., the styles 5–10, exserted for 1–2 mm, the internal receptacle surface velutinous, the short hairs simple, the pedicel 1.5–5 mm by 1–1.5 mm. Fruiting receptacles borne in clusters of 1–20 on leafy or leafless branches, ovoid to subglobose, 6–14 mm diam., externally pubescent with simple, stellate and fasciculate trichomes, the carpels 1–8 per receptacle, ovoid, 6–8 mm long, 4–6 mm wide, 4–5 mm thick, mucronate with a longitudinal crest, the endocarp thick, the surface deeply foveate, foveate-reticulate or foveate-sulcate.

Distribution. Endemic to Réunion (Fig. 22).

Habitat. Monimia rotundifolia is an occasional to locally abundant component of the cloud forest zone, rarely ranging into the *Philippia* heath zone, from ca. 1,000 to 2,000 m.

RÉUNION. BELOUVE: Apr. 1956 (fr), *Bosser 7586* (P); 1,500 m, Apr. 1956 (fr), *Bosser 9354* (P). BOIS DE NÈFLES: 1,500 m, 17 Sept. 1974 (fl), *Cadet 4787* (REU); (fl), *Cadet 4788* (REU); (fl), *Cadet 4789* (REU). BOUCAN-LAUNAY: woods above Boucan-Launay (fr), *Boivin 1120* (P). BRETAGNE: above Bretagne, 1,000 m, July 1945 (fr), *Rivals s.n.* (TL-R). BRÛLÉ DE ST. DENIS: 1,300 m, May 1957 (fl), *Bosser 11577* (P); 1,000 m, 22 Oct. 1973 (fr), *Bosser 21332* (P, 2 sheets); near Mamode Camp, 1,200 m, 13 Apr. 1968 (fr), *Cadet 1333* (REU); vicinity of Mamode Camp, at Plaine des Chicots, 31 Jan. 1968 (fr), *Capuron 28161-SF* (P, 2 sheets); St. Francois, St. Denis (fr), *Cordemoy s.n.* (TL-R); 1,000–1,200 m, Oct. 1956 (st), *Rivière s.n.* (P). BÉBOUR: Bébour Forest, 4,500 ft. (ca. 1,350 m), 17 Nov. 1967 (fl), *Barclay 554* (K, MAU); Bébour Pass and Rivière des Marsouins, 1,350 m, 21 Oct. 1973 (fl), *Bernardi 14530* (BM, G, P); Bébour Plateau, 1,200–1,300 m, June 1957 (fl), *Bosser 11488* (P, 2 sheets); 1,300 m, 27 Nov. 1973 (fl), *Cadet 4531* (REU); 26 Oct. 1974 (fl, fr), *Cadet 5197A* (REU); 29 May 1975 (fl), *Cadet 5197B* (REU); Bébour Peak, 1,700 m, 27 Nov. 1973 (fl), *Coode et al. 4231* (K, 2 sheets; REU); (fl), *Coode et al. 4235* (K); (fr), *Coode et al. 4237* (K, REU); (fl), *Coode et al. 4238* (K, 2 sheets; REU); 16 Dec. 1970 (fl, fr), *Friedmann 875* (P); 1,400 m, Nov. 1972 (fl, fr), *Friedmann 1982* (P); 1,300–1,600 m, 23 Feb. 1979 (fl), *Lorence 2429* (MO); 1,300 m, 6 May 1976 (fl), *Richardson et al. 4086* (K, MO); (fl), *Richardson et al. 4087* (K, MO); (fl), *Richardson et al. 4088* (K, 2 sheets; MO). CIRQUE DE CILAOS: Petit Matarum, 6 Mar. 1971 (fr), *Friedmann 1119* (P); Cilaos at Matarum, 1,300 m, June 1943 (fl), *Rivals s.n.* (TL-R). CIRQUE DE MAFATE: Sentier des Scouts, crest above Ilet à Malheur, 1,200 m, May 1976 (fr), *Richardson et al. 4138* (K, 2 sheets). CIRQUE DE SALAZIE: path from Grand Ilet to Roche Ecrite, 1,900 m, 15 Oct. 1974 (fl, fr), *Cadet 4836* (REU); below Grand Ilet at Salazie, 1,600 m, 26 Sept. 1977 (fl), *Cadet 5254* (REU); (fl), *Cadet 5255* (REU); Terre Plate, 1,600 m, 7 Apr. 1976 (st), *Cadet 5334* (REU). MAÏDO: road to Maïdo above Petit France, 1,200 m, 22 Feb. 1979 (fr), *Lorence & Cadet 2413* (MAU, MO); Maïdo to Le Guillaum road, 1,550 m, 12 May 1976 (fr), *Richardson et al. 4121* (K, MO); (fl), *Richardson et al. 4122* (K). MASSIF DE LA FOURNAISE: below the shelter at Pas de Bellecombe, 2,000 m, 25 July 1962 (fl), *Cadet 202* (REU). MORNE DE PATATES À DURAND: 1,200 m, Hauts du Bois de Nèfles à St. Denis, 11 Sept. 1976 (fl), *Cadet 5242* (REU); (fl), *Cadet 5243* (REU). PLAINE D'AFFOUCHES: June 1945 (fl), *Rivals s.n.* (TL-R). PLAINE DES CAFRES: open heathland, 5,200 ft. (ca. 1,700 m), 2 Aug. 1968 (fl), *Barclay 471* (K, MAU); Sentier Coteau Maigre, Feb. 1971 (fl, fr), *Bosser 20476* (P); Piton Mare a Bouc, 1,600 m, 7 Nov. 1966 (fl), *Cadet 503* (P, REU); foot of Piton Lepervanche, 1,700 m, 26 Oct. 1974 (fl), *Cadet 4859* (REU); Col de Bellevue, 30 Nov. 1974 (fl), *Friedmann 781* (P); (fl), *Friedmann 782* (P); Col de Bellevue, 1,600 m, 27 Feb. 1979 (fl, fr), *Lorence 2471* (MAU, MO); (fl), *Lorence 2472* (MAU, MO); (fl), *Lorence 2473* (MAU, MO); (st), *Lorence 2474* (MO); 17 July 1979 (fl, fr), *Lorence 2773* (MO, Z); (fl), *Lorence 2774* (K, MO, Z); (fl), *Lorence 2775* (K, MAU, MO, Z); base of Piton Bleu, 11 June 1943 (st), *Rivals s.n.* (TL-R); Grande Montée, mid and upper parts, 12 June 1943 (fl), *Rivals s.n.* (TL-R); lower part of forest at La Grand Montée, 1,200 m (st), *Rivals s.n.* (TL-R); scrub and cloud forest, 1,700 m, 5 Nov. 1966 (fl), *Schlieben 10859* (B, MAU); Grand Montée, 1,600 m, 28 May 1964 (fl), *Staub sub MAU 11105* (MAU); Grand Montée, 4,500 ft. (ca. 1,500 m), 10 Oct. 1960 (fl), *Wiehe sub MAU 1534* (MAU); 1,600 m, 27 Nov. 1964 (fl), *Wiehe sub MAU 11479* (MAU, 2 sheets). PLAINE DES CHICOTS: Roche Ecrite, 1,700–2,277 m, 8 Jan. 1975 (fl), *Bernardi 14936* (P); (fl), *Bernardi 14943* (P); Roche Ecrite, moist forest, 1,300 m, 23 July 1961 (st), *St. John 26527* (G, 2 sheets; K).

PLAINE DES MAKES: 1,100 m, June 1957 (fl), *Bosser 12216* (P); 1,400 m, 6 Apr. 1975 (st), *Cadet 5154* (REU). PLAINE DES PALMISTES: mountainous regions (fl), *Cordemoy s.n.* (TL-R); Petite Plaine above Plaine des Palmistes, 1,200 m, 25 Feb. 1979 (fr), *Lorence & Rolland 2453* (MO). PLAINE DES SALAZES: high altitude ericoid vegetation, Apr. 1957 (fr), *Alphonsine s.n.* (P). RIVIÈRE DE L'EST: far up the Rivière de l'Est, 1,750 m, Nov. 1976 (fl), *Cadet 5710* (REU); (fl), *Cadet 5711* (REU). RIVIÈRE DES REMPARTS: Roche Plate path, 6,500–6,700 ft. (ca. 2,100 m), 16 Nov. 1967 (fl), *Barclay 498* (K, MAU); ca. 5,400 ft. (ca. 1,700 m), 20 Nov. 1968 (fl, fr), *Barclay 1272* (K, MAU); Vallée de la Rivière des Remparts, 1,700 m, 20 Nov. 1968 (fl, fr), *Cadet 1727* (REU); 7 Mar. 1975 (fl), *Cadet 5103* (REU); (fr), *Cadet 5104* (REU); (fr), *Cadet 5105* (REU). SAINTE AGATHE: 19 July 1875 (fl), *De L'Isle 383* (K; P, 2 sheets). SAINTE MARIE: Hauts de Sainte Marie, 1,200 m, 18 Apr. 1976 (fl), *Cadet 5511* (REU). TAKAMAKA: 900 m, 10 Mar. 1979 (st), *Lorence & Rolland 2532* (MAU, MO). TÉVELAVE: Hauts du Tévelave, 1,500 m, 21 May 1975 (fr), *Bosser 22189* (P, 2 sheets); 1,300 m, 5 Sept. 1975 (fl), *Cadet 5255* (REU); ca. 1,500 m, 25 Nov. 1968 (fl), *Edgerley E4 sub MAU 13372* (MAU); May 1976 (fl), *Friedmann 2817* (P); forestry road above Tévelave, 1,300–1,400 m, 28 Feb. 1979 (fr), *Lorence 2477* (MAU, MO); 1,700 m, 6 Mar. 1979 (fl), *Lorence 2505* (MAU, MO); (fr), *Lorence 2506* (MAU, MO). WITHOUT PRECISE LOCALITY: (fl), *Anon. ex Herb. Kopp s.n.* (P, 3 sheets); (fl), *Anon. ex Herb. Station Agronom. Réunion s.n.* (P, 2 sheets); (fl), *Armange 20* (P); (fr), *Balfour s.n.* (K); (fl), *Barthe s.n.* (P); (fr), *Boivin 1120* (G, 2 sheets; P, 2 sheets); (fl, fr), *Boivin s.n.* (G; P, 3 sheets); (fl), *Bory de St. Vincent s.n.* (G-DC, microfiche); (fl), *Commerson s.n.* (BM, G, P; syntypes of *M. citrina*); (fl), *Commerson s.n.* (P); (fl), *De L'Isle s.n.* (P); (fl), *Gaudichaud s.n.* (G, P; syntypes of *M. rotundifolia*); (fl, fr), *Gaudichaud s.n.* (K, P); (fl), *Gaudichaud s.n. in 1837* (G); (st), *Giraudy s.n. in 1847* (P); (fl), *Monssi (?) s.n. in 1833* (P); (fl, fr), *Potier s.n.* (P, 3 sheets); (fl), *Richard 2* (K); (fl, fr), *Richard s.n.* (P, 3 sheets); (fl, fr), *Richard 27* (P, 2 sheets). LOCALITY (ISLAND) UNKNOWN: (fl), *Anon. sub Herb. ORSTOM 4999* (MAD); (fl), *Anon. sub MAU 2993* (MAU).

Monimia rotundifolia is an extremely variable species as to size and shape of the lamina, although its leaves are never sessile to subsessile and deeply cordate-amplexicaul as in *M. amplexicaulis.* Composition of laminar trichomes is also a variable feature. Long simple hairs predominate on the adaxial leaf surface of many individuals (e.g., Fig. 9C), but in others large numbers of long fasciculate and shorter stellate trichomes are present (e.g., Fig. 9B), approaching the condition found in *M. amplexicaulis.* Bojer (1837), followed by Baker (1877), erroneously stated that *M. rotundifolia* occurred in Mauritius, but cited no collections, and no authentic specimens are known from Mauritius. Its wood is occasionally used for construction in Réunion and is said to be virtually incombustible.

Vernacular names. Mapou, Mapou à grandes feuilles, Mapou blanc, Mapou des hauts (Réunion).

3. **Monimia ovalifolia** Thouars, Hist. Vég. Iles France 35, tab. 9, fig. 1. 1804; Thouars, Hist. Vég. Iles Austral. Afriq. 21, 34, tab. 7, fig. 1. 1805; Willd., Sp. Pl. 648. 1805; Spreng., Syst. 3: 906. 1825; Bojer, Hortus Maurit. 289. 1837; Poir., Encycl., Suppl. 3: 727. 1843; Tul., Monogr. Monim. 309. 1855; A.DC., Prodr. 16(2): 661. 1868; Baker, Fl. Mauritius 289. 1877; Cordem., Fl. Réunion 300. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 65, fig. 18E–F. 1901; Perk., Gatt. Monim. fig. 34E–F. 1925; Vaughan, Mauritius Inst. Bull. 1: 76. 1937. TYPE: Ile de France (Mauritius). Without precise locality (ca. 1800–1801), *Petit-Thouars s.n.* (lectotype, P, here designated; isolectotypes, P, 2 sheets).

M. ovalifolia var. *boryana* A.DC., Prodr. 16(2): 661. 1868. TYPE: without precise locality (probably Mauritius or Réunion) (ca. 1821), *Bory de St. Vincent s.n.* (holotype, G-DC, n.v.; microfiche, MO).

M. citrina sensu Cordem., Fl. Réunion 300. 1895 non Tul.

M. rotundifolia sensu Perk., Pflanzenr. 4, 101 (Nachtr.): 39. 1911 non Thouars, as to *Balfour s.n.* collection from Rodrigues (K).

Shrub or small tree 7–15 m tall and 40 cm diam., the bark pale brown, smooth, flaking, the new growth scurfy-pubescent, the mature leafy stems scurfy to scabrous, glabrescent, 2.5–5 mm diam., the stems, petioles, costa, and inflorescence axes scabrous to scurfy with mostly small, appressed stellate-peltate trichomes with 8–16 short, horizontal arms, mixed with fewer simple hairs and fasciculate trichomes with 2–8 long, ascendant arms. Leaves opposite, petiolate; petioles (3–)5–25 mm by 2–4 mm; lamina subcoriaceous to coriaceous, ovate-elliptic, elliptic, broadly elliptic, suborbiculate or orbiculate, occasionally obovate, (30–)50–130(–170) mm by (20–)30–110(–153) mm (attaining 200 mm by 200 mm with petioles 35 mm long on vigorous sucker shoots), the apex shortly acuminate, shortly acute, obtuse, rounded or retuse, the base acutely decurrent, acute, obtuse, rounded or shallowly cordate, the secondary veins 4–7 pairs, making a 50–65° angle with the costa, the venation depressed adaxially and visible to 2(–3°), raised abaxially and visible to 3(–4°), the adaxial laminar surface scabrous with scattered, ± ap-

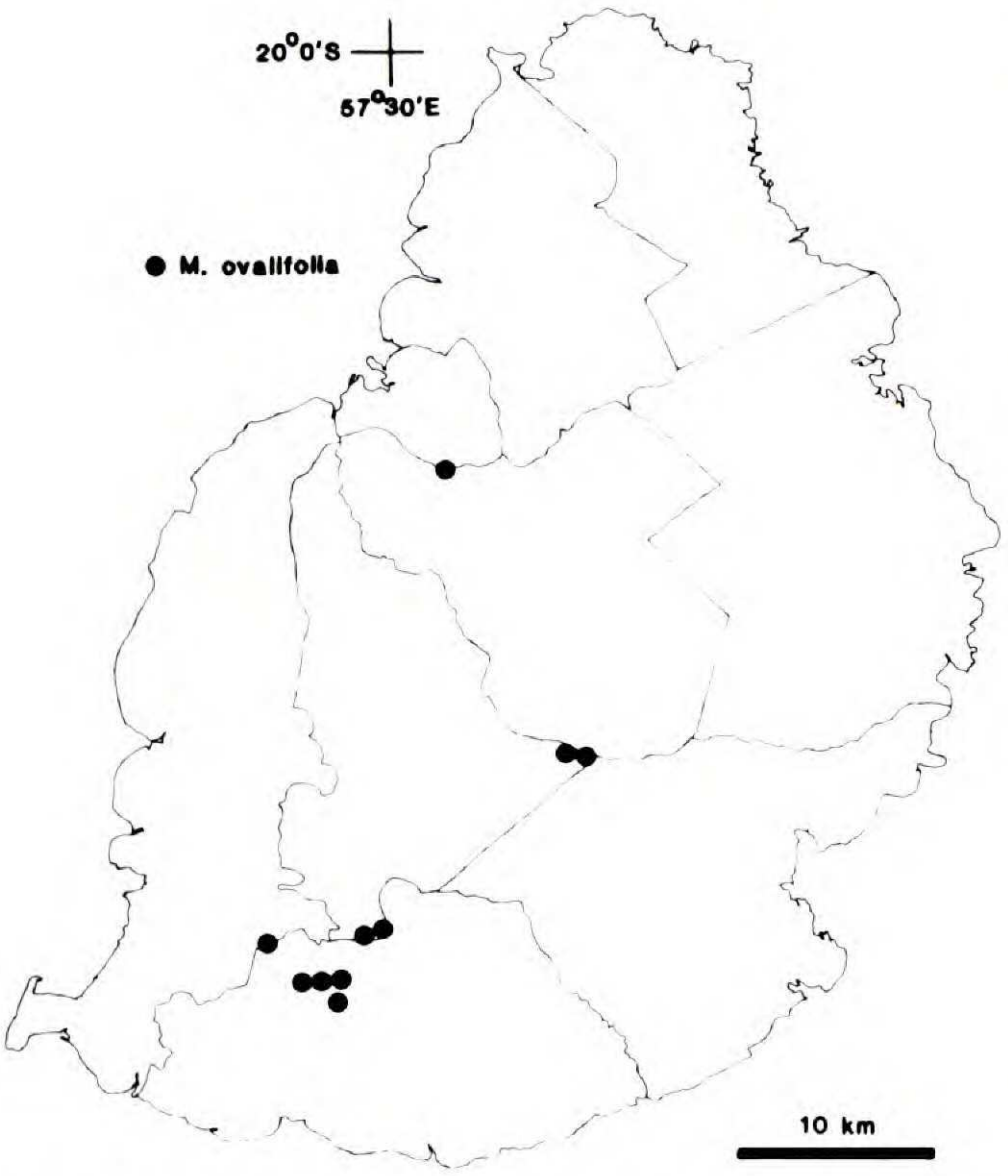

FIGURE 23. Distribution map of *Monimia* in Mauritius.

pressed stellate-peltate trichomes with 6–16 short, horizontal arms, the costa and secondary veins with scattered simple and fasciculate trichomes, eventually glabrescent and ± pustular, glandular, the abaxial laminar surface obscured by a dense whitish indument of the same trichomes, the margin entire, plane to slightly revolute. Inflorescence a scurfy to scabrous thyrse (rarely a short cyme or pleiochasium) of (3–)8–87 flowers, branching to 2(–3°), leafy or not, ramiflorous, either subfoliar on leafless nodes (the primary axis sometimes continuing to grow as a leafy stem), axillary, or rarely terminal, the floral axis (5–)10–120(–165) mm by 1.5–3 mm, often subtended by 1–several pairs of caducous brown, ciliate to pubescent naviculate bracts to 7 mm by 3 mm, the peduncle 3–20 mm by 0.5–1 mm, often subtended by a single caducous brown bracteole 2–5 mm long, or by a small leaf, bearing an umbelloid unit of (2–)3(–8) flowers. Androecious flower in bud ellipsoid to obovoid, 3–5 mm by 2.5–3 mm, the pedicel 1–7 mm by 0.3–0.6 mm, sometimes minutely bracteolate; at anthesis deeply 4–6-fid, 5–7 mm diam., the lobes reflexing; stamens ca. 45–60, 1.5–2 mm long, the anther ellipsoid, ca. 1 mm wide, comprising ca. ⅓–½ total length of the stamen, the connective rounded to apiculate, the internal receptacle surface pilose with short simple hairs. Gynoecious flower in bud ovoid-urceolate to subglobose-urceolate, 2.5–4 mm by 2.5–3.5 mm; at anthesis the orifice 0.6–0.8 mm diam., the styles 6–12, exserted for 0.5–1.5 mm, the internal receptacle surface velutinous with short simple hairs, the pedicel 1–4 mm by 0.5–1 mm. Fruiting receptacles borne on the leafy or leafless stems, in clusters of 1–20, ovoid to subglobose, 5–12 mm diam., the apex ± acuminate, externally scabrous with scattered stellate trichomes, the carpels 1–5 per receptacle, ovoid-compressed, 5–7 mm long, 4.5–5.5 mm wide, 3–4.5 mm thick, mucronate, with a longitudinal crest, the endocarp surface deeply foveate-sulcate.

Distribution. Endemic to the Mascarene Islands of Mauritius and Réunion (Figs. 22, 23).

Habitat. The species is occasional to locally common in lower montane wet and cloud forest in Réunion from ca. 500 to 1,700 m. In Mauritius, *Monimia ovalifolia* is known only from patches of cloud forest on the summits of Mts. Le Pouce, Cocotte, Lagrave, and Piton Grand Bassin (ca. 550–770 m), and also occurs in wet forest at Plaine Champagne (ca. 450 m).

MAURITIUS. BASSIN BLANC: path near Bassin Blanc, (fr), *Vaughan sub MAU 13081* (MAU). GRAND BASSIN: summit area, Piton Grand Bassin, ca. 700 m, 31 Jan. 1976 (fr), *Coode 4696* (K, 2 sheets); 18 Oct. 1978 (fl), *Lorence 1857* (MAU, MO); Chemin Cheval near Grand Bassin, 23 Jan. 1939 (fr), *Vaughan sub MAU 18546* (MAU). LE POUCE MT.: around summit, June 1860 (fl, fr), *Ayres s.n.* (K); at the upper limit of woods at the base of Mt. Pouce, 5 Sept. 1849 (fl), *Boivin s.n.* (P); (fl, fr), *Bojer s.n.* (K); base of the shoulder (fl), *Bouton s.n. in 1864–1865* (K); (fr), *Bouton s.n. in 1831* (P, 2 sheets); summit of the Pouce, highest part of the mountain (fl), *Bouton s.n.* (G-DC, n.v.; microfiche, MO); base of the shoulder (fl), *Bouton sub MAU 1307* (MAU); SE slope near the summit, 19 Nov. 1973 (fl), *Coode 4125* (K); ca. 30 m below summit on windward slope, 800 m, 14 Dec. 1978 (st), *Lorence 2145* (MO); 18 Aug. 1979 (fl), *Lorence 2910* (MO). MT. COCOTTE: mossy forest, summit, 10 June 1966 (fl), *Guého sub MAU 12175* (MAU, 2 sheets); indigenous vegetation along crest, 8 Nov. 1969 (fr), *Guého sub MAU 14130* (MAU, 2 sheets); summit, ca. 770 m, 1 Dec. 1978 (fl), *Lorence 1982* (K, MO); (fr), *Lorence 1983* (B, G, K, MAU, MO, P, REU, Z); 19 Dec. 1978 (st), *Lorence & Lecordier 2168* (MAU, MO, P); 17 Jan. 1979 (fr), *Lorence 2285* (MAU, MO); 29 Jan. 1979 (fr), *Lorence 2350* (MAU, MO); 10 Aug. 1979 (fl), *Lorence 2895* (MO); (fl), *Lorence 2896* (B, G, K, MAU, MO, P, REU, Z); 29 Jan. 1979 (st), *Lorence 2964* (MO). MT. LAGRAVE: dense thicket along crest, 27 Sept. 1969 (fl), *Guého sub MAU 14097* (MAU, 2 sheets); dense thicket on N flank, 27 Sept. 1969 (fl), *Guého sub MAU 14105* (MAU, 2 sheets); S slope facing Eau Bleue Reservoir, 620 m, 24 May 1979 (st), *Lorence & Lecordier 2650* (K, MAU, MO). PLAINE CHAMPAGNE: track from Plaine Champagne to Black River Gorges, 1,400 ft. (ca. 450 m), 4 Feb. 1975 (st), *Coode s.n.* (K). WITHOUT PRECISE LOCALITY: (fl), *Ayres s.n.* (MO, 2 sheets); (fr), *Bijoux sub MAU 1308* (MAU); (fr), *Bijoux sub MAU 1309* (MAU); (fr), *Bijoux sub MAU 1310* (MAU); (fl), *Boivin s.n.* (P, 2 sheets); (fl), *Bojer s.n.* (K); (fl), *Bouton s.n. in 1829* (K); (fl), *Bouton s.n.* (P, 2 sheets); (fl), *Ilardwicke s.n.* (G); (fl), *Neraud s.n.* (G); (fl), *Schledl s.n.* (P); (fr), *Vesco s.n. in 1850* (P, 2 sheets). RÉUNION. BASSE VALLÉE: Le Grand Coudé (above St. Joseph), 1,100 m, June 1957 (fl), *Bosser 12215* (P); heights of Basse Vallée, La Coudée, 22 Nov. 1973 (st), *Coode s.n.* (K); ravine of Basse Vallée, 25 Nov. 1970 (fr), *Friedmann 753* (P); Basse Vallée near St. Philippe, 900 m, 13 July 1979 (fl), *Lorence & Cadet 2726* (MO); (fl), *Lorence & Cadet 2727* (MAU, MO); 17 May 1976 (st), *Richardson 4152* (K); 17 Feb. 1956 (st), *Severin 50* (P, REU). BOIS BLANC: above Bois Blanc, 800 m, 8 Aug. 1972 (fl), *Cadet 3721* (REU); 800 m, Apr. 1972 (fl), *Friedmann 1884* (P). BÉBOUR FOREST: Bébour Peak (Piton Rond de Bébour), 1,300–1,600 m, 23 Feb. 1979 (fr), *Lorence & Cadet 2430* (MAU, MO); region of Bébour near Pl. des Palmistes, 19 Jan. 1975 (fr), *Bernardi 15171* (P). GRAND ÉTANG: 500 m, 15 July 1979 (fl), *Lorence & Rolland 2754* (MO); (fl), *Lorence & Rolland 2755* (MAU, MO); (fl), *Lorence & Rolland 2756* (MAU, MO); (fl), *Lorence & Rolland 2757* (MAU, MO). LANGEVIN: high valley of Langevin, 1,500 m, 10 May 1976 (fl), *Cadet 5400* (REU); valley to Langevin below Plaine des Sables, 1,400 m, 10 May 1976 (fl, fr), *Richardson 4106* (K). MORNE DES PATATES À DURAND: 1,200 m, Mar. 1973 (fr), *Friedmann 2199* (P). PLAINE DES CAFRES: bank of Rivière des Remparts, 1948 (fl), *Anon. s.n.* (probably *Rivals*) (TL-R); Grand Bassin at base of Piton Bleu, 11–12 July 1943 (fr), *Rivals s.n.* (TL-R); Grand Montée of the Plaine des Cafres, 1,300–1,500 m, 12 July 1943 (fl), *Rivals s.n.* (TL-R); Bank of Rivière des Remparts, Vallon Hoarau, 20 Oct. 1948 (fl), *Rivals s.n.* (TL-R). PLAINE DES PALMISTES: high plateaux, (fl, fr), *Cordemoy s.n.* (TL-R); Grande Montée, 1,400 m, roadside, 20 Dec. 1942 (fl, fr), *Rivals s.n.* (TL-R); (fr), *Rivals s.n.* (TL-R); Petite Plaine above Plaine des Palmistes, 1,200 m, 25 Feb. 1979 (fr), *Lorence & Rolland 2452* (MAU, MO). RIVIÈRE DES REMPARTS: Roches Plates path, 5,400 ft. (ca. 1,800 m), 20 Nov. 1968 (fl), *Barclay 1273* (K, MAU); high valley of Rivière des Remparts, 1,700 m, 20 Nov. 1968 (fl), *Cadet 1726* (REU); 1,650 m, 7 Mar. 1975 (fl), *Cadet 5106* (REU). ST. PHILIPPE (VICINITY): Mare Longue forest, 500 m, 25 Feb. 1975 (fr), *Cadet 5082* (REU); 1–2 Feb. 1968 (fr), *Capuron 28182-SF* (P, 2 sheets); 23 Nov. 1973 (fr), *Coode et al. 4176* (K, 2 sheets; MAU, REU); 25 Feb. 1975 (fr), *Coode 4954* (K, 2 sheets; REU); 2 Mar. 1979 (fr), *Lorence, Lorence & Cadet 2482* (MAU, MO); Mare d'Arzule, 500 m, Apr. 1944 (fr), *Rivals s.n.* (TL-R). TAKAMAKA: path from Takamaka towards Ilet à Bananes, 2,500 ft. (ca. 800 m), 18 Feb. 1968 (fr), *Barclay 1240* (K, MAU); rain forest, Tacamaca, 21 Dec. 1971 (fr), *Bosser 20926* (P); Takamaka forest, Ilet à Bananes, ca. 800–900 m, 10 Mar. 1979 (fr), *Lorence & Rolland 2531* (MO); ca. 1,000 m, 8 May 1976 (st), *Richardson et al. 4100* (K, MO). WITHOUT PRECISE LOCALITY: (fl), *Anon. ex Herb. Ventenat s.n.* (G); (st), *Anon. s.n.* (probably *Cordemoy*) (TL-R); (fl), *Frappier 269* (P); (fr), *Frappier 270* (P); (fl), *Frappier 271* (P). LOCALITY (ISLAND) UNKNOWN: (fl), *Anon. ex Herb. Richard 66* (P); (fl), *Anon. ex Herb. Richard s.n.* (P); (st), *Anon. sub Herb, Willd. 18080* (B, n.v.; microfiche, MO); "Madagascar" (probably Mauritius) (fl), *Colebrooke s.n.* (G); "Rodrigues" (probably Réunion) (fr), *Balfour s.n. in Aug.–Dec. 1874* (K).

Monimia ovalifolia differs from *M. amplexicaulis* and *M. rotundifolia* in having much sparser and uniquely short stellate-peltate laminar trichomes with the arms united basally for ca. ⅓–½ their length (Fig. 9D, E), flowers with much smaller receptacles, and in having tanniferous idioblasts in the petiolar cortex. Although characterized by a generally lower altitudinal range, *M. ovalifolia* occurs sympatrically with *M. rotundifolia* in many localities in Réunion (e.g., at Bébour), where both species remain distinct, apparently by temporal isolation of flowering.

Populations of *Monimia ovalifolia* from Réunion tend to have fewer simple and fasciculate trichomes on the stem, petiole, costa, and inflorescence. The leaves are larger than in Mauritius plants and more variable in shape, often obtuse or even orbiculate. Furthermore, crushed leaves of the Réunion plants usually produce a faint, citron-like odor not apparent in Mauritian plants, even though ethereal oil cells are present in the mesophyll of both. Intergradation of plants from the two islands is total, however, and formal recognition of infraspecific variants is impossible.

Vernacular name. Mapou (Réunion).

EXCLUDED SPECIES

Monimia lastelliana Baill., Bull. Mens. Soc. Linn. (Paris) 1: 342. 1882; Perk. & Gilg, Pflanzenr. 4, 101: 65. 1901. [= *Tambourissa lastelliana* (Baill.) Drake, see discussion under this species].

Decarydendron Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 34: 279. 1928; Cavaco, Bull. Soc. Bot. France 105: 38. 1958; Cavaco, Blumea Suppl. 4: 28, fig. 1. 1958; Cavaco in Humbert, Fl. Madagascar 80: 8, fig. II:1–8. 1959. TYPE: *D. helenae* Danguy.

Monoecious treelets or small trees 4–8 m tall, the trunk sometimes swollen basally, the new growth velutinous to canescent, the hairs simple or in fascicles of 2. Leaves opposite, petiolate, adaxially glabrescent, abaxially ± pubescent especially along costa and major veins, the venation festooned brochidodromous, the margin serrate to dentate; juvenile and sucker leaves unknown. Inflorescence cauliflorous, sometimes produced at the swollen base of the trunk, or

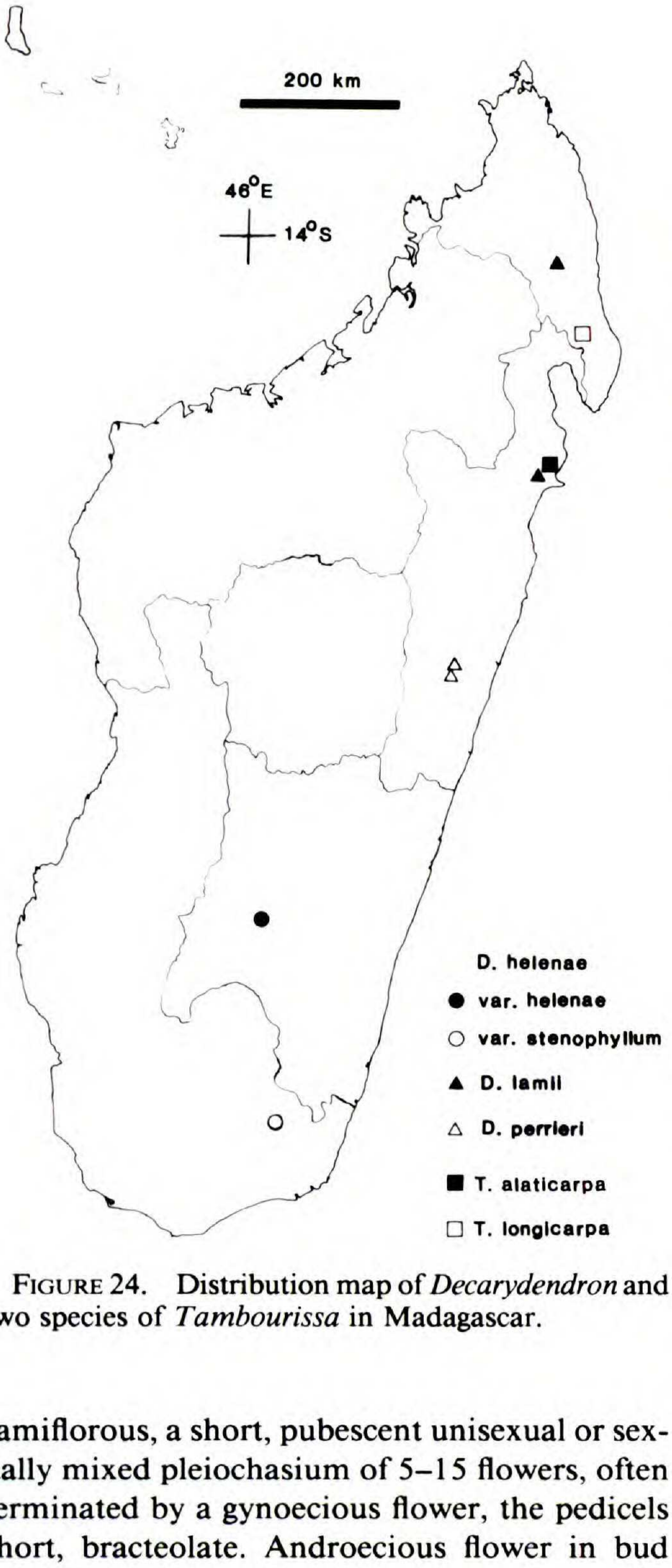

FIGURE 24. Distribution map of *Decarydendron* and two species of *Tambourissa* in Madagascar.

ramiflorous, a short, pubescent unisexual or sexually mixed pleiochasium of 5–15 flowers, often terminated by a gynoecious flower, the pedicels short, bracteolate. Androecious flower in bud subglobose to napiform, pubescent, the tepals imbricate, opening gradually, not splitting, at anthesis shallowly cupuliform to hemispherical, the rim bearing 10–15 large, subequal, broadly obtuse, radially arranged tepals in 1–2 series; stamens eglandular, 16–60, situated on the ± glabrous inner receptacle surface, the filament slender, distinct, the anther ovoid-ellipsoid, tetrasporangiate, the 2 loculi lateral, separate, longitudinally dehiscent, extrorse, the connective small, scarcely or not prolonged; pollen inaperturate, spheroid to subovoid, the sexine corrugate to rugulate, the sexinous elements short, finger-like. Gynoecious floral receptacle subglobose in bud, expanding gradually, not splitting, at anthesis broadly obconical to turbinate, ± angular, the walls fleshy, the rim bearing 9–15 broadly obtuse, radially arranged tepals, often eventually caducous, the carpels numerous, ca. 300–1,000, free, lining the receptacle, subsessile, clavate, ca. 1.5–2 mm long, ± polyhedral, the small stylar canal situated laterally in the basal half, the solitary ovary unilocular, the small loculus confined to the base of the carpel, containing a single pendulous, anatropous ovule, the carpels interspersed with ± dense, short simple hairs. Fruiting receptacle, mature carpels, and chromosome number unknown.

The genus was named after the French botanical explorer, R. Decary, who collected in Madagascar during the early part of the twentieth century.

Distribution. The three described species of *Decarydendron* are endemic to the wet evergreen forest zones of central and eastern Madagascar (Fig. 24).

TAXONOMIC HISTORY OF *DECARYDENDRON*

The genus *Decarydendron* was described by Danguy (1928) based on the species *D. helenae.* Thirty years later Cavaco (1958a, 1958b), described two additional species, *D. perrieri* and *D. lamii,* as well as another variety of *D. helenae,* var. *stenophyllum,* in preparation for his treatment for the "Flore de Madagascar" (1959). Herbarium material is scarce, and many additional flowering and fruiting collections and field observations are required for a meaningful revision of the genus.

SYSTEMATIC POSITION OF *DECARYDENDRON*

Decarydendron possesses the greatest constellation of primitive characters of any of the Malagasy Monimiaceae genera, notably the broad, shallowly concave floral receptacles with many large, whorled imbricate tepals, the numerous free, subsessile clavate carpels, and the cupuliform androecious flowers which expand gradually without splitting into segments as in the other genera (Fig. 14E). These features readily distinguish *Decarydendron* from the other two Madagascan genera which form an increasingly specialized series. *Decarydendron* resembles *Hedycarya* from Oceania in a number of respects, including the gynoecious floral morphology. Its mature fruiting receptacle presumably resembles that of the latter genus in having numerous sessile carpels situated on a flat, discoid receptacle.

Money et al. (1950) placed *Decarydendron* in the subfamily Monimioideae with the other Madagascan genera. Hutchinson (1964) placed it in the tribe Hedycaryeae within the same subfamily on the basis of its free, sessile carpels. In redefining the Monimioideae to include only *Monimia* and *Peumus,* Thorne (1974) created a new subfamily, the Mollinedioideae, to house the remaining genera formerly included in the Monimioideae. *Decarydendron* is therefore now included in the Mollinedioideae. As its pollen and vegetative and floral anatomy correspond most closely with the other members of this subfamily, I agree with its placement there.

KEY TO THE SPECIES OF *DECARYDENDRON*

1a. Leaves abaxially velutinous; petioles 3–5 mm long; tepals of androecious flowers crenulate .... 1. *D. perrieri*

1b. Leaves abaxially glabrate or at most puberulent; petioles 10–20 mm long; tepals of androecious flowers entire, not crenulate.

  2a. Laminar teeth 2–4 mm long; androecious flowers with 40–60 stamens .... 2. *D. helenae*

  2b. Laminar teeth 0.5 mm long; androecious flowers with 16–26 stamens .... 3. *D. lamii*

1. Decarydendron perrieri Cavaco, Bull. Soc. Bot. France 105: 38. 1958; Cavaco in Humbert, Fl. Madagascar 80: 9, fig. II:6–8. 1959. TYPE: Madagascar. Tamatave: Analamazaotra forest (near Perinet) (fl), *Perrier de la Bâthie 10089* (holotype, P).

Monoecious treelet or small tree 5–8 m tall, the base of the trunk swollen, the new growth densely velutinous, the mature leafy stems tomentose. Leaves opposite to subopposite, petiolate; petioles sparsely tomentose, 3–5 mm by 1.5–2 mm; lamina sparsely tomentose adaxially, velutinous abaxially, chartaceous, narrowly elliptic to narrowly ovate, 80–165 mm by 35–65 mm, the apex acuminate, the base broadly cuneate to obtuse, the secondary veins 5–7 pairs, making a 55–65° angle with the costa, depressed adaxially, the venation visible to 3° adaxially, to 4° abaxially, finely reticulate, prominent, the margin serrate-dentate with 30–35 pairs of subequal, acuminate teeth 1–3 mm long. Inflorescence cauliflorous at the swollen base of the trunk, sometimes extending up the trunk for some distance, a velutinous pleiochasium of 5–7 flowers, either unisexual of androecious flowers or sexually mixed and terminated by a gynoecious flower, the floral axis 120–220 mm by 3–4 mm, the pedicels 5–17 mm by 1.5–3 mm, basally bracteolate. Androecious flowers smaller than the gynoecious, the receptacle thick, externally velutinous, cupuliform, 7–14 mm diam., the margin bearing 10–18 subequal thick, deltoid-ovate or suborbicular tepals 5–6 mm long by 4–5 mm wide in two series, the external ones crenulate, the internal ones sinuate; stamens ca. 25, glabrous, 2–3 mm long, ellipsoid, the filament short, not prolonged, the anther ovoid, occupying ⅔ total length of the stamen. Gynoecious flower at anthesis externally velutinous, cupuliform, thick, 14–17 mm diam., with two longitudinal external ridges, each terminated by an ovate-acuminate, denticulate bracteole, the tepals subequal, deltoid to ovate, 3–6 mm by 5–7 mm, numbering 12–15, in two whorled series, the outer ones externally velutinous, the inner ones glabrate; carpels numerous, ca. 800–1,000, lining the receptacle, free, clavate, ca. 1.5 mm long. Fruiting receptacle unknown.

Distribution. Endemic to Madagascar (Fig. 24).

Habitat. The species is known only from the type locality, where it occurs in *Tambourissa/Weinmannia* wet forest at ca. 900 m.

MADAGASCAR. TAMATAVE: Perinet forest, 900 m, 30 Mar. 1974 (fl), *Cremers 3017* (MAD).

In addition to the characters cited in the key, *Decarydendron perrieri* differs from its congeners by the presence of a series of smaller tepals alternate with the larger outer series in the female flowers. Further collections, including fruiting material, and field observations are required to further assess its affinities within the genus.

2. Decarydendron helenae Danguy, Bull. Mus. Nat. Hist. (Paris), Ser. 1, 34: 279. 1928; Cavaco in Humbert, Fl. Madagascar 80: 10. 1959. TYPE: Madagascar. Fianarantsoa: forest at N base of Ivohibé Peak, 20 Sept. 1926 (fl), *Decary 5391* (holotype, P).

Small monoecious tree 7 m tall and 25 cm diam., the new growth golden tomentose, the mature leafy stems glabrescent, the trichomes simple or in fascicles of 2. Leaves opposite, petiolate; petioles 10–18 mm by 1.5–2.5 mm, glabrate; lamina ovate-elliptic to narrowly obovate-elliptic, 150–200 mm by 50–130 mm, chartaceous, adaxially hirsutulous when young, glabrescent, abaxially hirsutulous, velutinous along the costa and veins, the apex acute to shortly and abruptly acuminate, the base narrowly cuneate to obtuse, the secondary veins 5–8 pairs, making a 50–70° angle with the costa, the venation visible to 3° adaxially, to 4° abaxially, the margin prominently serrate-dentate, the teeth 15–25 pairs, unequal, acute to acuminate, 2–4 mm long, the glandular tips indurated. Inflorescence probably cauli- or ramiflorous, a finely velutinous pleiochasium of 5–7 flowers, unisexual of androecious flowers, or sexually mixed and terminated by a gynoecious flower, the floral axis 130–230 mm by 3–4 mm, the pedicels 10–15 mm by 1–1.5 mm, flattened near the junction with the receptacle, basally bracteolate. Androecious flower at anthesis cupuliform to hemispherical, 12–25 mm diam., the margin bearing a single series of 7–15 unequal, obtuse tepals 3–8 mm long by 6–10 mm wide, pilose on both surfaces; stamens ca. 40–60, glabrous, ellipsoid, 3–4.5 mm long, the filament ca. 0.5 mm long, the connective thick, not prolonged, the anther 2.5–4 mm long. Gynoecious flower larger than the androecious, at anthesis the receptacle broadly obconic to cupuliform, 15–35 mm long by 20–40 mm wide, externally pilose-velutinous, the margin bearing a single series of 8–15 thick, obtuse tepals 2–5 mm long by 2–4 mm wide; carpels numerous, up to 300 or more, lining the receptacle, clavate, 1.5–2.5 mm long, glabrous, interspersed with numerous short, simple trichomes. Fruiting receptacle and mature carpels unknown.

Distribution. Endemic to Madagascar (Fig. 24).

Decarydendron helenae differs from its congeners in having a combination of adaxially glabrate or only sparsely puberulent leaves with large marginal teeth, and more numerous stamens (up to 60 per flower). The species, particularly the variety *stenophyllum,* appears to be most closely allied to *D. perrieri.* More numerous collections and field studies are required to critically assess its status.

KEY TO THE VARIETIES OF
DECARYDENDRON HELENAE

1a. Leaves 90–130 mm wide; tepals ca. 15 .... 2a. var. *helenae*
1b. Leaves 50–75 mm wide; tepals 7–10 .... 2b. var. *stenophyllum*

2a. **Decarydendron helenae** var. **helenae.**

Variety *helenae* differs primarily in having larger leaves, a more robust inflorescence, and larger flowers than var. *stenophyllum.* Also, its receptacle lacks the two lateral ridges present in the latter variety. It was named after Helen Decary, who assisted her husband in his botanical research.

Habitat. Known only from the type, which was collected at the base of Ivohibé Peak in the Andringitra Massif in southern central Madagascar, it probably occurs in montane evergreen wet forest, most likely in the upper limits of the *Tambourissa/Weinmannia* zone (Fig. 24).

2b. Decarydendron helenae var. **stenophyllum** Cavaco, Bull. Soc. Bot. France 105: 39. 1958; Cavaco in Humbert, Fl. Madagascar 80: 10. 1959. TYPE: Madagascar. Tulear: upper basin of the Mandrare River (SE), pass and summit of Marosoui, 1,000–1,400 m, forest on gneissic laterite, 14–15 Nov. 1928 (fl), *Humbert 6613* (holotype, P; isotypes, K, MAD, US).

In addition to its narrower leaves, variety *stenophyllum* has a less robust inflorescence, smaller flowers with fewer tepals, and floral receptacles with two prominent, lateral ridges ending in small bracteoles. Whether these differences are constant or merely represent stages within a range of variation can only be ascertained by additional collections and field studies. The only known (type) collections of the varieties are, however, geographically separated by about 250 km.

Distribution. Endemic to Madagascar (Fig. 24).

Habitat. Variety *stenophyllum* is known only from the southeastern part of Madagascar, probably in the *Tambourissa/Weinmannia* wet forest zone.

3. Decarydendron lamii Cavaco, Blumea Suppl. 4: 28, fig. 1. 1958; Cavaco in Humbert, Fl. Madagascar 80: 12, fig. II:1–5. 1959. TYPE: Madagascar. Tamatave: Soanierana-Andasibé, 10 Dec. 1938 (fl), *Lam & Meeuse 5835* (holotype, presumably BO, n.v., photo, P; isotype, P).

Small monoecious understory tree 5 m tall, the new growth fulvous-velutinous, the mature leafy stems villous, 3–5 mm diam. Leaves opposite, petiolate; petioles 10–20 mm by 1.5–2 mm, velutinous; lamina chartaceous, narrowly elliptic to narrowly obovate-elliptic, 100–190 mm by 40–72 mm, the apex abruptly short acuminate, the base cuneate, the adaxial surface glabrate, the abaxial surface appressed pilose, especially on the costa and veins, the secondary veins 10–12 pairs, making a 65–75° angle with the costa, raised on both surfaces, the venation visible to 3° adaxially and to 4° abaxially, the margin plane, finely dentate, the teeth 40–50 pairs, 0.5 mm long, glandular tipped. Inflorescence cauliflorous from meristematic swellings on the trunk or ramiflorous, a pleiochasium of 8–15 flowers, unisexual of androecious flowers or sexually mixed and terminated by a single gynoecious flower, the floral axis 100–220 mm by 2 mm, densely fulvous-velutinous. Androecious flowers smaller than the gynoecious, at anthesis shallowly cupuliform to disciform, open, 12–16 mm diam. by 5–8 mm long, externally finely strigose-sericeous, the margin bearing 10–12 entire, obtuse, ovate to ligulate tepals 2–3 mm wide and long, in two series, the pedicel 6–25 mm by 1 mm, basally bracteolate, the bracteole to 4 mm long; stamens 16–26, ellipsoid to obovoid, 1.8–3 mm long by 1.5–1.8 mm wide, the filament distinct, short, the anther occupying ⅔–¾ total length of the stamen, the connective thick, not prolonged, the internal receptacle surface glabrous, purple. Gynoecious flower at anthesis obconical, 30 mm diam. by 24 mm long, externally finely velutinous, the carpels numerous (probably ca. 500 or more), lining the receptacle. Fruiting receptacle and mature carpels unknown.

Distribution. Endemic to Madagascar (Fig. 24).

Habitat. The species is known from the lower montane wet forest zone of Myristicaceae/*Anthostema* in the eastern region, below 900 m.

MADAGASCAR. DIEGO SUAREZ: S slope of Betsomanga, Bassin of Androranga River, 700 m, 18 Nov. 1950 (fl), *Capuron 827-SF* (P). TAMATAVE: Andapa District, eastern slopes of the Marojejy Massif, Lokoho River basin, E of Ambalamansy II, 450–800 m, rain forest on gneissic laterite, 28 Nov. 1948 (st), *Humbert & Capuron 22154* (MO).

In addition to the characters cited in the key, *Decarydendron lamii* differs from its congeners in that the androecious flowers are purple within. Like the other species in the genus, it is poorly known.

Ephippiandra Decne., Ann. Sci. Nat. (Paris), Ser. 4, 9: 278, pl. 7. 1858; A.DC., Prodr. 16(2): 662. 1868; Baill., Hist. Pl. ed. 1, 1: 304. 1869; Perk., Engl. Bot. Jahrb. 25(4–5): 551, t. 5: 1–5. 1898; Perk. & Gilg, Pflanzenr. 4, 101: 50, fig. 9. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 15. 1911; Perk., Gatt. Monim. 32, fig. 19. 1925; Cavaco, Bull. Soc. Bot. France 104: 610. 1957; Cavaco in Humbert, Fl. Madagascar 80: 4. 1959; Hutch., Gen. Fl. Pl. 1: 117. 1964. TYPE: *E. myrtoidea* Decne.

Hedycaryopsis Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 34: 278. 1928, synon. nov. TYPE: *H. madagascariensis* Danguy.

Monoecious shrubs, treelets or trees 10–25 m tall, the trunk attaining 50 cm diam., the new growth pubescent to glabrate, the hairs simple. Leaves opposite to subopposite, petiolate, subglabrous or ± pubescent abaxially, especially along the costa and veins, the venation festooned brochidodromous, semicraspedodromous or craspedodromous, the margin entire or sparsely dentate apically with acute, glandular teeth, or sinuate-dentate with rounded, apically depressed glandular teeth; juvenile and sucker leaves unknown. Inflorescence axillary, terminal, or ramiflorous on leafless stems, a short, 5-flowered unisexual pleiochasium or a 3–5-flowered sexually mixed dichasium, the gynoecious flower solitary and terminal, maturing first, the androecious flowers lateral, or the flowers solitary and axillary, the pedicels ± long and slender, basally bracteolate. Androecious flower in bud globose to ellipsoid, bearing 2–4(–5) small tepals apically, at anthesis splitting deeply into 4(–5) ± regular valvate segments, these spreading flat or reflexing, the apex often bearing 1–2 obtuse, scale-like tepals internally; stamens eglandular, ca. 9–50, situated irregularly or in several series on the glabrous to puberulent internal receptacle surface, ligulate to shortly deltoid, the filament broad, short or sessile, the anther tetrasporangiate, the 2 loculi lateral and separate or connivent or confluent apically, longitudinally dehiscent, extrorse; pollen inaperturate, spheroid to ovoid, the exine thick, the sexine granulate with few to many, small to large scattered verrucae or gemmae. Gynoecious flower in bud subglobose-discoid, concave, the margin usually bearing 4–8(–16) small, decussate deltoid tepals; at anthesis expanding gradually, not splitting, broadly obconic to discoid, the torus flat to concave, bearing ca.

15–120 free, short sessile, 4–6-sided columnar carpels ca. 1–1.5 mm long, the apex flat, the small stylar canal lateral, medial, the ovary unilocular, the solitary ovule anatropous, situated in a small locule near the base of the carpel, the carpels interspersed with short, simple hairs. Fruiting receptacle discoid, enlarged, fleshy and red when fresh, the flat to convex surface bearing ca. 10–75 free carpels, each surrounded basally by a cupule for ⅓–½ its length; mature carpels ovoid to ellipsoid, 7–12 mm long, the thin fleshy mesocarp ripening black, the endocarp thin, horny, pale brown, the surface scrobiculate, the endosperm fleshy. Chromosome number unknown.

Distribution. All six species are endemic to Madagascar (Figs. 25, 26).

Habitat. The genus ranges from lower montane wet and cloud forest to high altitude montane sclerophyllous forest and ericoid formations.

TAXONOMIC HISTORY OF *EPHIPPIANDRA*

The genus *Ephippiandra,* described by Decaisne in 1858 based on *E. myrtoidea,* was named in reference to the low, saddle-shaped anthers characteristic of the species. A second species, described by Perkins (1911) as *Tambourissa microphylla,* was subsequently transferred to *Ephippiandra* by Cavaco (1957a). In the same year Cavaco (1957c) described a third species and established two sections in the genus based on the presence (section *Staminodia*) or absence (section *Ephippiandra*) of fleshy tepals on the inner tips of the receptacle lobes, which he referred to as "staminodes."

Danguy described *Hedycaryopsis* in 1928 based on *H. madagascariensis,* and Cavaco (1958c) subsequently described three additional species preceding his treatment for "Flore de Madagascar" (1959).

GENERIC DELIMITATIONS AND SYSTEMATIC POSITION OF *EPHIPPIANDRA*

Danguy (1928) established *Hedycaryopsis* as a segregate genus primarily on the basis of its gynoecious flowers, which he felt approached those of *Hedycarya* Forst. (syn. *Carnegieodoxa* Perk.) from Oceania. The discoid to broadly obconic gynoecious flowers of *Hedycaryopsis,* like those of *Ephippiandra,* are usually bordered by several pairs of minute, decussate deltoid tepals and the torus bears few to numerous free, sessile polyhedral-columnar carpels on its surface (15–38 in *Ephippiandra*; 22–120 in *Hedycaryopsis*; Fig. 14F, G). Furthermore, carpels of both possess oblique lateral stylar canals (Fig. 13C, D). Danguy apparently never examined gynoecious flowering material of *Ephippiandra,* because he makes no mention of it in his discussion (the type of *E. myrtoidea* has only androecious flowers and fruit). Clearly, gynoecious floral morphology does not support segregation of *Hedycaryopsis* from *Ephippiandra.*

Furthermore, fruiting receptacles of both genera are morphologically identical. Mature fruiting receptacles in both consist of a fleshy, discoid torus, red when ripe, bearing few to many ovoid to ellipsoid carpels surrounded basally by cupules (Fig. 14H). Carpels of both have a thin mesocarp, green when fresh, overlying the thin, horny endocarp. Understandably, fruiting characters have never been used to distinguish the genera.

Although Danguy (1928) noted that androecious flowers of *Hedycaryopsis* scarcely differed from those of *Tambourissa,* Cavaco (1957c, 1959) felt that stamens were a stable key character separating *Ephippiandra* from *Hedycaryopsis* and *Tambourissa.* He stated that in *Ephippiandra* the stamens were sessile and broader than long ("déprimées") with the loculi apically confluent into a single, crescentiform loculus, as opposed to *Hedycaryopsis* which had separate, lateral loculi and an apically prolonged connective. He ignored, or at least failed to mention, however, that in species such as *E. myrtoidea* the loculi may be both connivent as well as confluent in the same flower. *Tambourissa* displays the entire range of conditions and the loculi may be separate, connivent, or confluent not only apically but basally as well in various species. Two or more of these conditions may occur in a single androecious flower of *T. cordifolia* (Fig. 42C–E). Other species such as *T. purpurea* possess broad, sessile stamens with a single loculus similar to those of some *Ephippiandra* species. Furthermore, the number of stamens is relatively small in both and overlaps (10–36 in *Ephippiandra*; 9–26 in *Hedycaryopsis*), as does the presence or absence of tepals on the extremities of the receptacle lobes. Androecious floral morphological characters are therefore clearly insufficient for generic segregation.

Examination of the pollen of two species each of *Ephippiandra* and *Hedycaryopsis* (Lorence, 1980; Lorence et al., 1984) has revealed that their sexinous patterns correspond much more closely to each other than to any of the other Malagasy genera. Pollen of *E. microphylla* and *E. myrtoidea* both have thick, granulate to verrucate sexines with larger, scattered gemmae and folds occurring in the latter. In *H. perrieri* and *H. tsaratanensis* the sexine is also thick and granulate with large, dome-shaped verrucae and gemmae. Sexinous patterns in these two genera differ primarily in the size of the processes, but correspond much more closely to each other than to the remaining Malagasy genera. I do not feel that pollen supports separation of the two genera.

Cavaco (1959) further distinguished these genera on the basis of inflorescence structure: dichasial with a central gynoecious flower and lateral (rarely solitary) androecious flowers in *Hedycaryopsis* (Fig. 14F, G); solitary or pleiochasial in *Ephippiandra*. The only species supposedly having pleiochasia, *Ephippiandra capuronii*, actually belongs in *Tambourissa* (see below). Collections of *E. myrtoidea* (*Anon. sub Herb. ORSTOM 3366*, MAD; *Anon. sub Herb. Alaotra 300*, MAD) possess sexually mixed dichasia, however, thus undermining the validity of this character in separating the genera. Furthermore, an even greater range of inflorescence types occurs in the otherwise very cohesive genus *Tambourissa*.

Leaves of the various *Hedycaryopsis* species are extremely diverse and display a striking array of venation patterns (see section on Leaf Architecture). For example, leaves of the type species, *H. madagascariensis*, are highly specialized and generally characterized by open craspedodromous venation ending in sunken teeth at the sinuate-dentate margin (Fig. 6F), a pattern apparently derived from the brochidodromous condition (R. Keating, pers. comm.). In this respect, they differ strikingly from all other known Monimiaceae genera and may have influenced Danguy (1928) to describe the genus as new. Venation in two other species, *H. capuronii* (= *Ephippiandra domatiata*; Fig. 6C, D) and *H. tsaratanensis* (Fig. 6E), as well as some collections of *H. madagascariensis*, is transitional between craspedodromous and brochidodromous, thus linking it to *H. perrieri* (Fig. 6B) which has festooned brochidodromous venation typical of virtually all other genera of Monimiaceae, including *Ephippiandra myrtoidea* (Fig. 6A) and *E. microphylla*. This intergrading range of venation patterns provides another criterion for uniting the two genera.

Because there seems to be no basis for continued segregation of *Hedycaryopsis*, I propose that it be reduced to synonymy under *Ephippiandra*, which would thus encompass six species, necessitating one new name and three new combinations given below.

Among the Malagasy Monimiaceae belonging to the Mollinedioideae, *Ephippiandra* occupies a position intermediate between *Decarydendron* and *Tambourissa* in terms of floral morphological specialization. The strong androecious/gynoecious floral dimorphism, highly reduced tepals, sessile carpels enveloped basally by cupules in fruit, androecious receptacle closed in bud and splitting open at anthesis, and tendency towards short, sessile stamens with confluent loculi are all specializations over *Decarydendron*. Female floral construction in *Ephippiandra* is not so advanced as in *Tambourissa*, however, where the closed gynoecious receptacle splits partly open at anthesis and the carpels are inferior and syncarpous.

KEY TO THE SPECIES OF *EPHIPPIANDRA*

1a. Leaf margin sinuate-dentate with rounded, apically ± depressed teeth.
  2a. Abaxial laminar surface densely ferrugineous tomentose; floral pedicel 25–50 mm long, ferrugineous tomentose .... 1. *E. tsaratanensis*
  2b. Abaxial laminar surface at most grayish or yellowish puberulent along costa and veins; floral pedicel 8–15 mm long, grayish canescent or villous .... 2. *E. madagascariensis*
1b. Leaf margin entire or at most with 1–2 pairs of acute, deltoid teeth in apical portion.
  3a. Basal pair of secondary veins extending up to or beyond middle portion of lamina before joining next pair above; barbate domatia present abaxially in secondary vein axils .... 3. *E. domatiata*
  3b. Basal pair of secondary veins joining next pair above before attaining middle of lamina; domatia absent abaxially in secondary vein axils.
    4a. Apex of lamina retuse, folded downward into a thickened flap .... 4. *E. perrieri*
    4b. Apex of lamina shortly acuminate to acute or rounded, not retuse or thickened into a flap.
      5a. Inner portion of each androecious floral receptacle lobe bearing 1(–2) scale-like tepals .... 6. *E. microphylla*
      5b. Inner portion of androecious floral receptacle lobes lacking scale-like tepals .... 5. *E. myrtoidea*

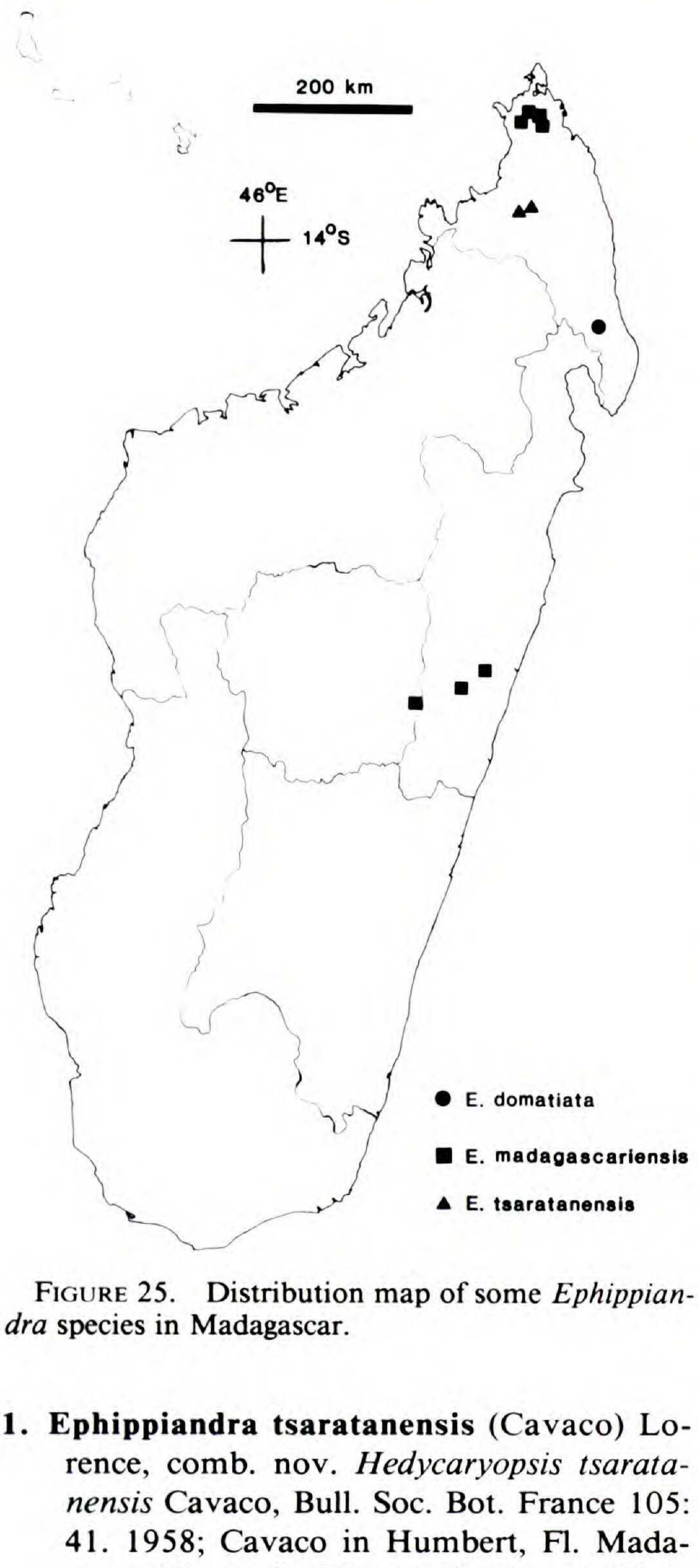

FIGURE 25. Distribution map of some *Ephippiandra* species in Madagascar.

1. **Ephippiandra tsaratanensis** (Cavaco) Lorence, comb. nov. *Hedycaryopsis tsaratanensis* Cavaco, Bull. Soc. Bot. France 105: 41. 1958; Cavaco in Humbert, Fl. Madagascar 80: 14, fig. III:1–5. 1959. TYPE: Madagascar. Diego Suarez: Tsaratanana Massif, forest with herbaceous undergrowth, 1,800 m (fl), *Perrier de la Bâthie 15302* (holotype, P).

Monecious tree 10–25 m tall, the new growth densely ferrugineous tomentose, the mature leafy stems sparsely tomentose. Leaves opposite to subopposite, petiolate; petioles 8–15 mm by 2.5–3.5 mm, ferrugineous tomentose; lamina subcoriaceous, the apex rounded, obtuse, the tip depressed, the base broadly cuneate, rounded, truncate or rarely subcordate, adaxially pubescent, glabrescent, abaxially densely ferrugineous tomentose, the secondary veins 5–8 pairs, making a 50–65° angle with the costa, the venation craspedodromous or partly brochidodromous, visible to 3° adaxially, to 4° abaxially, the margin slightly revolute, sinuate with 5–8 pairs of broadly rounded, apically depressed teeth. Inflorescence axillary, ferrugineous velutinous, a 3–5-flowered, sexually mixed dichasium, the 2–4 androecious flowers lateral, the gynoecious flower terminal and maturing first, the peduncle 15–30 mm by 2–3 mm, apically dialated, the pedicels each subtended by a linear bracteole 4–6 mm long. Androecious flower in bud ellipsoid to globose, 4–6 mm diam., ferrugineous tomentose, bearing near the apex 4 linear-ovate tepals 3–4 mm long, the pedicel 25–50 mm by 1 mm; at anthesis deeply 4-fid, 12–15 mm diam., the lobes spreading flat, each bearing a broad tepal apically within; stamens 18–20, ovate to ligulate, 2–2.5 mm long by 1–1.5 mm wide, slightly incurved, the filament thick, short or sessile, the loculi lateral, separate, occupying almost entire length of the stamen, the connective slightly prolonged, apiculate. Gynoecious flower at anthesis broadly obconical, concave, externally ferrugineous tomentose, 14–18 mm wide by 7–8 mm long, the margin bearing several minute, deltoid tepals, the pedicel 32–37 mm long; carpels 40–70, lining the receptacle, columnar, 4–5-sided, 1–1.5 mm long. Mature fruiting receptacle red when fresh, drying dark brown, irregularly discoid, convex, 60–85 mm diam., the ground tissue containing numerous stone cells, bearing (4–)40–70 free carpels surrounded basally by cupules for ⅓–½ their length, the pedicel and peduncle ca. 45 mm long by 3–4 mm diam.; mature carpels ovoid-ellipsoid, 10–12 mm long by 6–7 mm diam., green when fresh, drying brown, the mesocarp thin, fleshy, the endocarp whitish, 0.2 mm thick, the surface scrobiculate.

Distribution. Endemic to Madagascar (Fig. 25).

Habitat. The species is known only from the type locality on the Tsaratanana massif in north central Madagascar where it occurs from ca. 1,800 to 2,500 m, presumably in montane sclerophyllous cloud forest.

MADAGASCAR. DIEGO SUAREZ: Tsaratanana massif, trail up S ridge of Maromokotro, Andohanisambirano, 2,000–2,500 m; montane cloud forest, 9 May 1974 (fl, fr), *Gentry 11605* (MO).

The species is most closely allied to *Ephippiandra madagascariensis,* from which it differs by its suborbicular, abaxially ferrugineous tomentose leaves with mixed craspedodromous/brochidodromous venation, its more densely ferrugineous tomentose parts, more robust inflorescence with longer pedicels subtended by long, linear bracteoles, and by its androecious buds bearing 4 long, linear-ovate tepals.

2. **Ephippiandra madagascariensis** (Danguy) Lorence, comb. nov. *Hedycaryopsis madagascariensis* Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 34: 278. 1928; Cavaco in Humbert, Fl. Madagascar 80: 14, fig. IV:1–6. 1959. TYPE: Madagascar. Diego Suarez: Antsalaky forest, 700–1,000 m, 17 Oct. 1927 (fl, fr), *Ursch 66* (lectotype, P, here designated).

Monoecious tree 10–25 m tall and 50 cm diam., the new growth grayish to yellowish pubescent or canescent, the mature leafy stems 3–5 mm diam., puberulent. Leaves opposite to subopposite, petiolate; petioles puberulent, 8–15 mm by 1.5 mm; lamina subcoriaceous, ± bullate, obovate-elliptic to suborbicular, 30–90 mm by 22–60 mm, the apex obtuse, rounded, the tip retuse, the base cuneate, the adaxial surface sparsely puberulent, glabrescent, the abaxial surface puberulent, especially along the costa and veins, the secondary veins 3–5 pairs, making a 40–50° angle with the costa, depressed adaxially, prominent abaxially, dichotomizing and running into the marginal teeth, the venation craspedodromous, rarely semicraspedodromous, visible to 2° adaxially, to 3° abaxially, the margin revolute, sinuate with 2–7 pairs of broadly obtuse, apically depressed teeth. Inflorescence axillary, a sexually mixed, 3–5-flowered dichasium, the 2–4 androecious flowers lateral, subtending the terminal gynoecious flower, or the gynoecious flower rarely solitary, the peduncle grayish pubescent, 15–30 mm by 1–1.5 mm, apically dilated. Androecious flower in bud globose, 3–4 mm diam., the canescent pedicel 8–20 mm by 0.6–0.8 mm, each subtended by a naviculate bracteole 2 mm long, the apex bearing 3–4 obtuse, puberulent tepals 1–2 mm long; at anthesis deeply 4(–5)-fid, ca. 10 mm diam., the lobes spreading flat; stamens 35–50, ligulate-subulate, 1.5–2 mm long by 0.7 mm wide, the filament thick, subsessile, the loculi lateral, separate, occupying almost entire length of the stamen, the connective thick, prolonged, obtuse, the internal receptacle surface glabrous. Gynoecious flower at anthesis discoid, flat, 10–15 mm diam. by 1.5 mm thick, externally canescent, the margin bearing 8 or 16 minute, deltoid tepals 0.5 mm long, the pedicel canescent, 6–15 mm by 1.5 mm; carpels ca. 140–150, lining the receptacle, sessile, columnar, 5–6-sided, 0.8–1 mm long by 0.6–0.8 mm wide, the apex flat, interspersed with numerous short, simple hairs, the internal receptacle surface with mucilaginous secretion. Mature fruiting receptacle swollen, everted, 35–60 mm diam., bearing 30–50 carpels, the pedicel and peduncle ca. 25 mm by 3 mm; carpels ovoid-ellipsoid, 8–10 mm long by 6–7 mm diam., the basal ¼–⅓ enveloped by a cupule, the mesocarp reddish, fleshy, ca. 0.5 mm thick, the endocarp brown, foveolate-reticulate.

Distribution. Endemic to Madagascar (Fig. 25).

Habitat. Ephippiandra madagascariensis appears to be primarily restricted to the *Tambourissa/Weinmannia* wet forest zone (ca. 700–1,000 m) in northern and eastern Madagascar.

MADAGASCAR. DIEGO SUAREZ: Montagne d'Ambre, S of Les Roussettes Forestry Station by Petit Lac and above on the summit, 1,100–1,200 m, 22 Dec. 1967 (fl), *Bernardi 11977* (K, MO); Montagne d'Ambre National Park, mature wet forest, ca. 1,200 m, 23 May 1974 (fr), *Gentry 11962* (MO); Montagne d'Ambre, Dec. 1964 (st), *Morat 1182* (MAD, P); 1,100 m, 7 Dec. 1952 (st), *Schedl 170* (MAD); (st), *Schedl 177* (MAD). TAMATAVE: Beandy, Perinet, 12 Sept. 1948 (fl), *Anon. sub Service Forestier 1596-SF* (MAD); Analamazaotra forest (Perinet), 1919 (fr), *Thouvenot s.n.* (P, syntype of *Hedycaryopsis madagascariensis*); road from Anosibé to Moramanga, 9 May 1969 (st), *Anon. sub Service Forestier 26852-SF* (MO, P). TANANARIVE: Ahimiadana Canton, Andramasina, forest SE of Lake Tsiazompaniry, May 1961 (fl), *Capuron 20278-SF* (MO).

The species is most closely allied to *Ephippiandra tsaratanensis,* differing by its obovate, abaxially glabrous or sparsely puberulent leaves with open dichotomous, craspedodromous (rarely partly brochidodromous) venation, its yellowish to grayish canescent pubescence, and less robust inflorescence with shorter pedicels, bracteoles, and androecious tepals. It yields a yellowish wood said to be good for construction.

Vernacular names. Ambora, Amborabé, Tambonaika (Madagascar).

3. **Ephippiandra domatiata** Lorence, nom. nov. *Hedycaryopsis capuronii* Cavaco, Bull. Soc. Bot. France 105: 40. 1958; Cavaco in Hum-

bert, Fl. Madagascar 80: 13. 1959 non *Ephippiandra capuronii* Cavaco, Bull. Soc. Bot. France 104: 610. 1957. TYPE: Madagascar. Diego Suarez: Beanjada Massif (N of the Masoala Peninsula), ridge at ca. 1,100 m, 30 Dec. 1953 (fl), *Capuron 8828-SF* (holotype, P).

Monoecious shrub, the new growth with sparse, scattered hairs, glabrescent, the mature leafy stems 1–2 mm diam., becoming lenticellate. Leaves opposite, petiolate; petioles glabrous, 6–10 mm by 0.7–1 mm; lamina glabrous, chartaceous, obovate-elliptic to rhombic, 25–40 mm by 14–25 mm, the apex obtuse to retuse, often apiculate, the base cuneate, the secondary veins 2–3 pairs, the strong basal pair making a 40–45° angle with the costa, attaining top half of the lamina before uniting brochidodromously with the next pair, adaxially depressed, abaxially prominent, the axils of the basal veins domatiate and barbate abaxially, the venation visible to 2° adaxially and to 3–4° abaxially, the margin revolute, with 1–2(–3) pairs of minute teeth in the apical ½–⅓. Inflorescence axillary, a 3-flowered dichasium, the terminal gynoecious flower subtended by 2 androecious flowers, or the male flowers solitary or in cymes of 3, the peduncle glabrous, (4–)12–15 mm by 0.5 mm, with 2 basal bracteoles. Androecious flower in bud globose, 2.5–3 mm diam., glabrous, the apex with 2 pairs of broadly obtuse tepals 1.5–2 mm wide, the pedicel 7–8 mm by 0.5 mm, subtended by a bracteole 1–1.5 mm long; at anthesis deeply 4-fid, 5–6 mm diam., the lobes spreading flat, each bearing apically 2 thin, broadly obtuse tepals internally; stamens 9–10, ovoid-subulate, 1–1.5 mm long by 0.6–0.8 mm wide, the filament short, distinct, the loculi lateral, separate, occupying ca. ¾ total length of the stamen, the connective slightly prolonged, apiculate. Gynoecious flower at anthesis discoid, flat, 4.5–5 mm diam. by 1.5 mm thick, externally with a few scattered hairs, the margin entire or with a few minute, deltoid teeth, the pedicel glabrous, 9–19 mm by 0.5 mm, occasionally basally bracteolate; carpels 24–25, sessile, columnar, 0.8 mm long by 0.6–0.7 mm wide, 5–6-angled, interspersed with tufts of short, simple hairs. Fruiting receptacle unknown.

Distribution. Endemic to Madagascar (Fig. 25).

Habitat. The species is known only from the type locality, presumably in *Tambourissa*/*Weinmannia* wet forest at ca. 1,100 m.

Ephippiandra domatiata is readily distinguishable from its congeners by its glabrous inflorescence and stems, and particularly by its leaves with abaxially domatiate, barbate secondary vein axils. Further collections, especially fruiting material, and field observations are greatly desired.

4. **Ephippiandra perrieri** (Cavaco) Lorence, comb. nov. *Hedycaryopsis perrieri* Cavaco, Bull. Soc. Bot. France 105: 40. 1958; Cavaco in Humbert, Fl. Madagascar 80: 16. 1959. TYPE: Madagascar. Diego Suarez: Tsaratanana massif, forest with herbaceous understory, 2,000 m, Apr. 1929 (fl, fr), *Perrier de la Bâthie 16249* (holotype, P).

Monoecious shrub, treelet or tree 12–15 m tall, the new growth finely cinereous pubescent, the mature leafy stems 2–3 mm diam., grayish puberulent, glabrescent, often with large, elliptic lenticels. Leaves opposite to subopposite, petiolate; petioles 5–11 mm by 1 mm, finely puberulent, glabrescent; lamina chartaceous to subcoriaceous, glabrous, elliptic to obovate or obcordate, 25–55 mm by 15–35 mm, the apex obtuse, rounded, the tip retuse or emarginate, folded under into a thickened flap, the base narrowly cuneate, the secondary veins 3–4 pairs, making a 45–55° angle with the costa, obscure adaxially, prominent abaxially, the venation visible to 3° adaxially and to 4° abaxially, the margin entire, ± revolute. Inflorescence axillary, a 3-flowered, sexually mixed dichasium, the gynoecious flower terminal, subtended by a pair of androecious flowers, or the androecious flowers solitary, axillary, the peduncle 10–15 mm by 1 mm, finely puberulent, subtended by several small, deltoid bracteoles. Androecious flower in bud globose, 3 mm diam., with scattered appressed hairs, the apex bearing 2 obtuse to subulate, ciliate tepals 1–1.5 mm long, the pedicel 8–20 mm by 0.7 mm, often with 1–2 minute bracteoles; at anthesis deeply 4–5-fid, 9–10 mm diam., the lobes spreading flat or recurving slightly, internally glabrous, each terminated by a broad, retuse or bifid tepal internally; stamens 15–20, recurved, 2–2.5 mm long, the filament slender, 1–1.5 mm long, the anther ovoid-ellipsoid, 1 mm long, the loculi lateral, separate, the connective prolonged, apiculate. Gynoecious flower on a pedicel 12–20 mm by 1 mm, bracteolate basally or medially, the receptacle open in bud; at anthesis flat, discoid, 4–6 mm diam. by 2 mm thick, externally finely gray sericeous, the margin bearing 4–8(–16) minute, deltoid tepals ca. 0.5 mm long; carpels 20–25, bluntly columnar, 1 mm long by 0.6–0.8 mm wide, 5–6-angled, covering the torus, interspersed with short, simple hairs. Mature fruiting receptacle swollen, 15–20 mm diam., usually with 2–4 carpels, the pedicel and peduncle 25–45 mm by 1.5 mm; carpels ovoid, 8–9 mm by 6–7 mm, the basal ¼–⅓ enclosed by a raised cupule, the mesocarp thin, fleshy, the endocarp light brown, striate-reticulate.

Distribution. Endemic to Madagascar (Fig. 26).

Habitat. The species is restricted to sclerophyllous montane cloud forest and ericoid formations on Madagascar's highest mountains, the Marojejy and Tsaratanana massifs, from ca. 2,000 to 2,650 m.

MADAGASCAR. DIEGO SUAREZ: Marojezy (Marojejy) massif, summit, 29 Mar. 1949 (fl, fr), *Anon. sub Herb Alaotra 3479* (MAD, 3 sheets); Marojejy Natural Reserve, sclerophyllous forest, 2,000 m, 27 Nov. 1972 (fl), *Guillaumet 4058* (MAD); ericoid scrub on the summit of Marojejy, 2,000–2,137 m, Dec. 1972 (fl), *Morat 4035* (MAD, P); Tsaratanana massif, 2,200–2,650 m, Nov. 1966 (fl), *Capuron 25000-SF* (MO, P); 2,100 m, Nov. 1966 (fr), *Morat 2268* (MAD, P); Andohanisambirano, 2,500 m, Nov. 1966 (fl), *Morat 2332* (MAD); (fr), *Morat 2333* (MAD).

Ephippiandra perrieri most closely resembles *E. domatiata,* but its leaves have entire margins, a more deeply retuse or emarginate apex which is thickened and folded under into a flap, lack domatia, and the inflorescence is sparsely pubescent. In sheltered forest *E. perrieri* becomes a tree, but takes on a shrubby habit on exposed slopes.

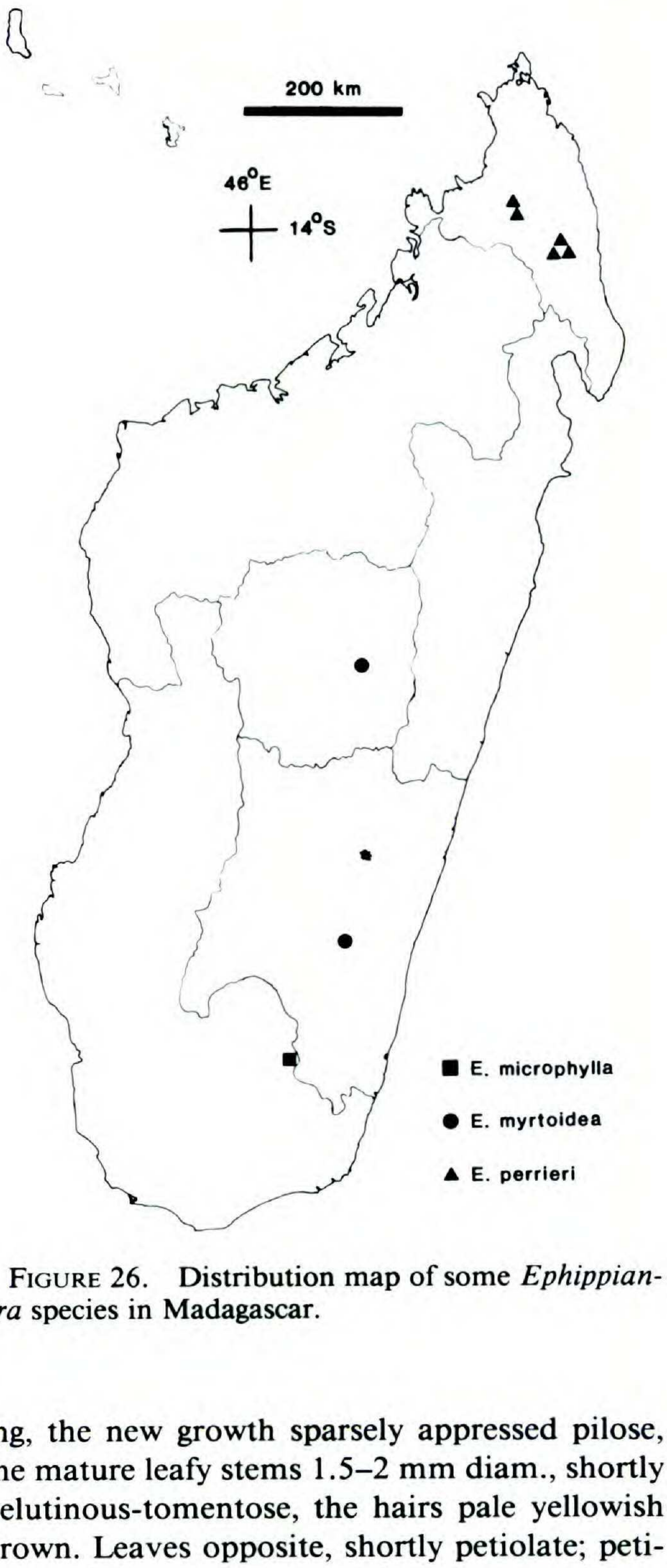

FIGURE 26. Distribution map of some *Ephippiandra* species in Madagascar.

5. **Ephippiandra myrtoidea** Decne., Ann. Sci. Nat. (Paris), Ser. 4, 9: 278, pl. 7. 1858; A.DC., Prodr. 16(2): 662. 1868; Baill., Hist. Pl. ed. 1, 1: 304. 1869; Perk., Engl. Bot. Jahrb. 25(4–5): 551, t. 5:1–5. 1898; Perk. & Gilg, Pflanzenr. 4, 101: 51, fig. 9. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 15. 1911; Perk., Gatt. Monim. 32, fig. 19. 1925; Cavaco in Humbert, Fl. Madagascar 80: 6, fig. I:7–9. 1959. *Mollinedia myrtoidea* (Decne.) Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902. TYPE: Madagascar. Tananarive: vicinity of Tananarive (fl), *Goudot s.n. in 1840* (holotype, P).

Monoecious treelet 3–4 m tall, densely branching, the new growth sparsely appressed pilose, the mature leafy stems 1.5–2 mm diam., shortly velutinous-tomentose, the hairs pale yellowish brown. Leaves opposite, shortly petiolate; petioles 1–5 mm by 1 mm, velutinous-tomentose; lamina chartaceous to subcoriaceous, ovate to elliptic, 12–30 mm by 8–22 mm, the apex acute to abruptly short acuminate, the tip thickened, the base cuneate to obtuse or rounded, adaxially with a few appressed hairs when young, abaxially with hairs along the costa and margin, the secondary veins 3–6 pairs, making a 65–85° angle with the costa, the venation obscure adaxially, visible to 2° abaxially, the margin entire, pilose, slightly revolute. Inflorescence axillary or terminal, a 3–5-flowered dichasium with a single terminal gynoecious flower subtended by 2–4 androecious flowers, or the flowers axillary, solitary or in cymes of 2–3, the peduncle 3–4 mm by 1 mm, pubescent, basally bracteolate. Androecious flower in bud globose, 2–4 mm diam., with scattered hairs, the apex apiculate with 1–2 pairs of small, obtuse tepals to 1 mm wide, the pedicel 2.5–20 mm by 0.6 mm, bracteolate; at anthesis deeply 4-fid, 6–8 mm diam., the lobes spreading flat, each usually terminated by a small, obtuse tepal externally; stamens 10–13, 2–3 per lobe, sessile, obtuse, 1 mm long by 1.5–2.5 mm wide, the loculi connivent or usually confluent apically into a single crescentiform loculus, the filament broad, short or sessile, the inner receptacle surface glabrous. Gynoecious flower on a pedicel 6–25 mm by 0.8 mm; at anthesis the receptacle discoid, flat or ± concave, 6–8 mm diam. by 1 mm thick, the surface crowded with 25–30 sessile, 4–6-sided columnar carpels 0.8–1 mm long by 0.7–0.9 mm wide, interspersed with short, simple hairs. Mature fruiting receptacle terminal, the torus swollen, convex, 15–30 mm diam., red when fresh, drying black, the surface sparsely pubescent, bearing (1–)3–14 carpels, the pedicel and peduncle 25–50 mm by 1.5–2.5 mm; carpels ovoid to ellipsoid, 8–9 mm by 5–6 mm, the basal ⅓–½ surrounded by a raised cupule, the mesocarp black when ripe, drying blackish, thin, fleshy, the endocarp thin, brown, the surface finely scrobiculate.

Distribution. Endemic to Madagascar (Fig. 26).

Habitat. The species appears to be restricted to the *Tambourissa/Weinmannia* montane sclerophyllous forest and high altitude ericoid zones of eastern and central Madagascar, from ca. 1,300 to 2,000 m.

MADAGASCAR. FIANARANTSOA: high valley of the Rienana (Basin of the Matitanana River), forest, 1,000–1,400 m, 18–22 Nov. 1924 (fl), *Humbert 3447* (K). PROVINCE UNCERTAIN: Manijarivolo-Andrianony, 1,650 m, 30 Oct. 1970 (fl), *Anon. sub Herb. ORSTOM 3366* (MAD); Central Madagascar (fl), *Baron 1263* (K); (fr), *Baron 1355* (K); Andrangaloatra (fr), *Parker s.n. in 1881* (K); Andohakelo Massif (R.N. 11), 1,800–1,850 m, Jan. 1974 (fl, fr), *Morat 4430* (P); *Morat 4434* (P); *Morat 4480* (P). WITHOUT PRECISE LOCALITY: (fl), *Anon. sub Herb. Alaotra 300* (MAD).

The species is virtually indistinguishable from *Ephippiandra microphylla* except for its androecious flowers which have fewer stamens and lack tepals on the inner apical portion of the receptacle lobes. Pedicel length and inflorescence type intergrade, and further collections and field studies are necessary to ascertain whether the taxa are distinct or merely represent variations of a single, polymorphic species.

6. **Ephippiandra microphylla** (Perk.) Cavaco, Kew Bull. 12: 228. 1957; Cavaco in Humbert, Fl. Madagascar 80: 7, fig. III:6–9. 1959. *Tambourissa microphylla* Perk., Pflanzenr. 4, 101 (Nachtr.): 41. 1911. TYPE: Madagascar. Province uncertain: Ambohimitombo forest (Tanala), 1,350–1,440 m, 22 Dec. 1894 (fr), *Forsyth-Major 326* (holotype, K).

Monoecious treelet or small tree 2–3 m tall, the new growth sparsely pilose to yellowish velutinous-tomentose, the mature leafy stems tomentose or glabrate, 2–3 mm diam. Leaves opposite to subopposite, petiolate; petioles pilose to tomentose, 2–5 mm by 1.2–2 mm; lamina chartaceous, ovate, elliptic or oblong, 20–50 mm by 10–25 mm, the apex acute to abruptly acuminate, the base cuneate to broadly cuneate or obtuse, the secondary veins 4–6 pairs, making a 60–75° angle with the costa, the venation scarcely visible to 2° adaxially, visible to 3° abaxially, the surfaces glabrous, the margin slightly revolute, entire or frequently bearing a pair of small, acute glandular teeth in the apical portion. Inflorescence axillary or terminal, the flowers solitary. Androecious flowers axillary, in bud globose to obovoid, 3–4 mm diam., subglabrous, the apex bearing 4 obtuse tepals, the pedicel 12–27 mm by 0.5 mm, basally bracteolate, subglabrous; at anthesis deeply 4-fid, ca. 10 mm diam., the lobes spreading flat, each bearing a broad, truncate tepal ca. 2 mm wide internally near the apex; staens 16–18, broadly deltoid to ovoid-obtuse, 1–2 mm long by 1.5–2 mm wide, the filament very short or sessile, the loculi confluent apically into a single crescentiform loculus, the connective thick, not prolonged, the internal receptacle surface glabrous. Gynoecious flower subglabrous externally, on a pedicel 20–25 mm by 0.8 mm; at anthesis discoid, flat to slightly concave, 5–6 mm diam., the surface bearing ca. 38 densely crowded, free sessile, 4–6-sided, columnar carpels 0.5 mm diam., interspersed with short, simple hairs. Mature fruiting receptacle enlarged, the torus 15–35 mm diam., bearing 15–25 carpels; carpels ovoid to ellipsoid, 7–8 mm by 4–5 mm, immersed basally in cupules for ca. ½ their length, the mesocarp thin, fleshy, the endocarp thin, brown.

Distribution. Endemic to Madagascar (Fig. 26).

Habitat. The species is known primarily from south central Madagascar where it occurs in the montane *Tambourissa/Weinmannia* wet forest zone from ca. 900 to 1,500 m, but also extends up into the sclerophyllous forest zone from ca. 1,300 to 2,000 m.

MADAGASCAR. TULEAR: Mt. Itrafanaomby (Ankazondrano) and its SW contreforts (high Mandrare basin), rain forest and ericoid scrub on gneissic crests, 1,600–1,963 m, end Dec. 1933 (fl), *Humbert 13518* (MO).

The species is most closely allied to *Ephippiandra myrtoidea,* from which it differs by its androecious flowers, which have more numerous stamens (16–18), and a single broad, truncate tepal on the inner extremity of each receptacle lobe.

EXCLUDED SPECIES

Ephippiandra capuronii Cavaco, Bull. Soc. Bot. France 104: 610. 1957 (= *Tambourissa beanjadensis* Lorence, see discussion under this species).

Tambourissa Sonn., Voy. Ind. Orient. ed. 1, 3: 267, tab. 134. 1782; ed. 2, 4: 405, tab. 134. 1806; Gmel., Syst. Nat. 2(1): 16. 1791, '*Tamburissa*' (sphalm.); A.DC., Prodr. 16(2): 658. 1868; Baill., Hist. Pl. ed. 1, 1: 341. 1869; ed. 2, 1: 332. 1871; Baker, Fl. Mauritius 287. 1877; Benth. & Hook., Gen. Pl. 139. 1883; Pax, Pflanzenfam. 3(2): 101. 1899; Cordem., Fl. Réunion 300. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 66. 1901; Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 39. 1911; Perk., Gatt. Monim. 44. 1925; Cavaco, Bull. Soc. Bot. France 104: 284. 1957; Cavaco in Humbert, Fl. Madagascar 80: 18. 1959; Hutch., Gen. Fl. Pl. 1: 118. 1964. TYPE: *T. quadrifida* Sonn.

Tamboure cissa Flacourt, Hist. Madagascar 133, pl. 69. 1661 (pre-Linnaean polynomial).

Mithridatea Comm. ex Schreb., Gen. Pl. 2: 783. 1791; Willd., Sp. Pl. 1(1): 27. 1797; Spreng., Syst. 5(3): 866. 1826, nom. nov. for *Tambourissa* Sonn.

Ambora Juss., Gen. Pl. 401. 1789; Juss., Ann. Mus. Hist. Nat. (Paris) 14: 130. 1809; Poir., Encycl. 7: 565. 1806; Tabl. Encycl. 784. 1806; Steud., Nom. Bot. 37. 1821; Endl., Gen. Pl. 4(2): 56. 1842; Tul., Ann. Sci. Nat. (Paris) 4(3): 29. 1855; Tul., Monogr. Monim. 295. 1855, nom. nov. for *Tambourissa* Sonn.

Schrameckia Danguy, Bull. Mus. Hist. Nat. (Paris) 28: 249. 1922; Perk., Gatt. Monim. 45. 1925; Metay, Arch. Bot. Bull. Mens. 3(11): 177. 1929; Cavaco, Bull. Soc. Bot. France 105: 39. 1958. TYPE: *S. madagascariensis* Danguy (= *Tambourissa floricostata* Cavaco).

Phanerogonocarpus Cavaco, Bull. Soc. Bot. France 104: 612, figs. 1–4. 1957; Cavaco in Humbert, Fl. Madagascar 80: 2, fig. I:1–6. 1957, synon. nov. TYPE: *P. capuronii* Cavaco (= *Tambourissa longicarpa* Lorence).

Small to moderate sized monoecious or dioecious trees, treelets or shrubs, ± aromatic. Leaves simple, usually opposite and decussate, rarely clustered into pseudoverticels, or ternate to alternate, glabrous or pubescent with simple, rarely fasciculate, unicellular trichomes, the margin entire to serrate-dentate with glandular teeth, the venation festooned brochidodromous, the juvenile and sucker leaves usually heterophyllous, apically serrate-dentate. Inflorescence terminal, axillary, ramiflorous or cauliflorous, sometimes leafy, the axes bracteolate, the flowers solitary, fasciculate or disposed in dichasia, pleiochasia or thyrses; flower in bud fleshy, globose, globose-depressed, cylindrical to obovoid, urceolate or napiform (the gynoecious bud usually flattened or depressed apically), apiculate, the apex with several pairs of minute decussate tepals extending into the orifice; male receptacle at anthesis usually splitting into (3–)4–6(–7) ± regular, valvate segments, these remaining partially closed or usually spreading flat and ± reflexing; stamens eglandular, few to very numerous, multiseriate, situated on the glabrous or rarely hairy internal receptacle surface, the anthers tetrasporangiate, bilocular, the 2 loculi free and lateral, connivent, or confluent apically or rarely basally, longitudinally dehiscent, extrorse, sessile or with a distinct filament, the connective sometimes prolonged apically; pollen inaperturate, spheroid to ovoid, the sexine striato-reticulate to rugulate, granulate or granular-tectate; female receptacle at anthesis cylindrical, napiform, cupuliform or rarely discoid, the orifice generally 4(–10)-lobed or entire, the lobes reflexing or not; carpels numerous, immersed in and fused with the receptacle wall, the styles free and protruding, setose or conical to columnar, the internal receptacle surface frequently bearing simple hairs, in some species producing a copious mucilaginous exudate, the ovary unilocular, the ovule solitary, pendulous, anatropous to amphitropous. Fruiting receptacle cupuliform, subglobose, urceolate or cylindrical, corky brown externally, the fruiting carpels (drupes) enclosed within the accrescent receptacle wall which splits open irregularly at maturity; carpels ovoid-compressed, surrounded by a fleshy, oily red-orange mesocarp, the endocarp horny, whitish to black, the surface smooth or variously sculptured, the embryo straight, the cotyledons flat, oval to elliptic. Gametic chromosome number: $n = 19$.

Distribution. *Tambourissa* is a genus of about 43 species restricted to the southwest Indian Ocean islands of Madagascar (26 spp.), the Comores (5 spp.), the Mascarene Islands of Mauritius (10 spp.), and Réunion (2 spp.). The species display a high degree of endemism, each being restricted to a given island and frequently to a specific habitat within the island.

Habitat. Species of *Tambourissa* are occasional to locally common components of evergreen moist, wet, and cloud forest formations, often conspicuous because of their peculiar flowering and fruiting receptacles.

TAXONOMIC HISTORY OF *TAMBOURISSA*

The name *Tambourissa,* adopted from the pre-Linnaean polynomial "Tamboure cissa" (presumably derived from "tamboul," a Malagasy term for testicles) employed by Flacourt (1661), was first validly published by Sonnerat in 1782. Sonnerat based his genus *Tambourissa* on a single species, *T. quadrifida,* which he undoubtedly described and illustrated while in Mauritius (Ly-Tio-Fane, 1976). A genus characterized by peculiar, often large, cupuliform or urceolate to cylindrical fruiting receptacles containing numerous immersed carpels, *Tambourissa* goes by the colorful local appellations of "Bois tambour" (drumwood) or "Pot de chambre jacot" (monkey's chamber pot) in Mauritius. In neighboring Réunion it is called "Bois de bombarde" (bombardment wood) because the ripe fruiting receptacle splits open irregularly to reveal an array of numerous, red-orange carpels set against the pale orange receptacular pulp (Fig. 17B). In Anjouan and Grand Comore (Comore islands) *Tambourissa* is known as "M'bweza," meaning to calm or sooth the pain, because its leaves are used medicinally in tea. Many species in Madagascar and Mayotte (Comores) go by the name of "Ambora." The species in Mohéli is called "Diarou."

Sonnerat felt the genus occupied a position somewhere between *Ficus* and *Dorstenia* because of its closed, fig-like buds and gynoecious floral receptacle with an inferior, syncarpous gynoecium. In 1789, the genus was redescribed by A. L. de Jussieu as *Ambora* from the Malagasy vernacular name, and again as *Mithridatea* by Commerson, Sonnerat's mentor, in Schreber (1791). It is unclear why these authors redescribed *Tambourissa* under other names, because both genera were based on Sonnerat's original species, *T. quadrifida.* It was not until 1855 that Tulasne correctly placed the genus in Monimiaceae, publishing 11 new species of *Ambora* (1855a) for his monograph of the family (1855b).

In 1868, Alphonse de Candolle transferred all of Tulasne's species to *Tambourissa,* describing no new taxa but providing one new name. Baker (1877) described two new species of *Tambourissa* from Mauritius in his treatment of the family for "Flora of Mauritius and the Seychelles" and later described three more from Madagascar. At the turn of the century, Perkins and Gilg (1901) monographed the entire family for Engler's "Pflanzenreich," providing a synoptic treatment for *Tambourissa* and describing one new species. In her revision of the family ten years later, again for the "Pflanzenreich," Perkins (1911) published four additional species from the Comores and Madagascar. During this same period, Drake del Castillo (1902) published two new species, and Danguy (1922) published another (as *Schrameckia* because of its few, large stamens), all from Madagascar. After a hiatus of some 35 years, Cavaco revised the Malagasy Monimiaceae for "Flore de Madagascar et des Comores" (1959), publishing nine new Malagasy species of *Tambourissa* (1957a, 1957c, 1957d, 1957e, 1958c). Most recently, Lorence (1982) published seven new species and one subspecies of *Tambourissa* from the Malagasy region. *Phanerogonocarpus,* described by Cavaco (1957c), was named for its narrowly winged, tubular gynoecious flowers and fruits and based on two Madagascan species. In the present revision of *Tambourissa,* three new names are proposed, and at the same time nine other taxa are reduced to synonymy.

GENERIC DELIMITATIONS AND SYSTEMATIC POSITION OF *TAMBOURISSA*

The genus *Phanerogonocarpus* was described by Cavaco (1957b) on the basis of its winged or ribbed, narrowly obconical to cylindrical gynoecious flowering and fruiting receptacles (Fig. 17A), which he compared to the ribbed flowers of *Schrameckia.* Cavaco (1959) later undermined this character when he reduced *Schrameckia* to synonymy under *Tambourissa.* Furthermore, two species of *Tambourissa, T. perrieri,* and *T. quad-*

rifida, both possess ellipsoid to obovoid gynoecious floral receptacles approaching those of *Phanerogonocarpus,* although not as narrow. Carpels of both genera are identically immersed in and united with the receptacle wall (Figs. 13E, 16A–D). Furthermore, styles of *Phanerogonocarpus* are conical with an acute apex, possess an oblique stylar canal, and are interspersed with short simple hairs as in *Tambourissa* (Fig. 16D).

Fruiting receptacles of both genera are externally corky brown and split open irregularly at maturity to reveal the numerous ripe carpels immersed in a pale orange matrix. That the fruit of *Phanerogonocarpus* splits lengthwise leaving the central tube more or less intact is related to its elongated shape; the ellipsoid to obovoid fruits of *Tambourissa quadrifida* behave similarly. Mature fruiting carpels of both genera consist of a bright orange, fleshy mesocarp enclosing the dark brown, finely sculptured endocarp. Supposed differences between the genera in gynoecious floral and fruit morphology are clearly those of degree and fail to support generic segregation.

In his original description of *Phanerogonocarpus,* Cavaco (1957c) noted the resemblance of its androecious flowers and stamens to those of *Tambourissa,* except for the presence of tepals ("staminodes") on the inner tips of the receptacle lobes in the former. This feature is, however, shared with a number of *Tambourissa* species such as *T. comorensis, T. floricostata,* and *T. paradoxa* to name a few. Cavaco correctly interpreted the staminal morphology of *Phanerogonocarpus* as falling within the range of variability displayed by *Tambourissa,* however.

Pollen of *Phanerogonocarpus capuronii* (= *Tambourissa longicarpa*) is subspheroid to ovoid with a striato-rugulate sexine composed of short, compactly spaced finger-like elements. That of *P. perrieri* (= *T. alaticarpa*) is spheroid to subovoid with a rugulate sexine composed of more continuous elements than in *P. capuronii.* Sexinous patterns of both species are strikingly similar to those found in many *Tambourissa* species, e.g., *T. comorensis, T. cordifolia, T. ficus, T. floricostata,* and *T. quadrifida.* A survey of pollen from a range of *Tambourissa* species shows the genus to have sexinous sculpturing ranging from striato-reticulate or rugulate to granular-tectate, thus readily accommodating the patterns displayed by *Phanerogonocarpus* (Lorence et al., 1984).

Regarding inflorescence structure, the sexually mixed pleiochasium terminated by one or two gynoecious flowers in *Phanerogonocarpus* (Fig. 17A) also occurs in a number of *Tambourissa* species, e.g., *T. hildebrandtii* and *T. perrieri.* Finally, leaf architecture of the two genera overlaps. Adult leaves of a number of *Tambourissa* species, e.g., *T. thouvenotii* and *T. trichophylla,* as well as juvenile and sucker leaves of many species are dentate, as are adult leaves of *Phanerogonocarpus.* I can find no obvious basis for maintaining *Phanerogonocarpus* as a distinct genus and therefore propose that it be reduced to synonymy under *Tambourissa.*

Tambourissa has attained the highest level of floral morphological specialization of all the Malagasy Monimiaceae in the subfamily Mollinedioideae. Most species are characterized by a strong androecious/gynoecious floral dimorphism, have flowers of both sexes closed in bud, have highly reduced tepals, show a range of staminal specialization via reduction and, most significantly, the gynoecious flowers have their carpels immersed in and fused with the massively developed ovary wall, with the fruiting carpels likewise enclosed in the accrescent receptacle which splits open irregularly at maturity.

INTRAGENERIC RELATIONSHIPS

Tambourissa, with about 43 species, is the largest genus of Monimiaceae in the Old World. Its members often display extensive interspecific variation in floral morphology (color, size, shape, and number of parts), pubescence, leaf morphology, and other characters. Even species which are obviously closely related with respect to features such as foliar and gynoecious floral morphology may differ radically and inexplicably in other features such as androecious floral or staminal morphology. This happens frequently enough to render the establishment of meaningful subgeneric categories such as subgenera or sections impossible at present. I have, therefore, chosen to place the species into informal groups of morphologically similar taxa to facilitate their comparison, but no phylogenetic implications are intended by this sequence. Nine species groups are listed below, each followed by a discussion (refer also to Tables 5–7):

1. Group A. ..... *Tambourissa thouvenotii, T. trichophylla, T. uapacifolia*
   Group B. ..... *Tambourissa decaryana, T. hildebrandtii, T. hum-*

		bertii, T. nitida, T. nosybensis
	Group C.	*Tambourissa floricostata, T. parvifolia*
2.	Group A.	*Tambourissa beanjadensis, T. comorensis, T. crassa, T. elliptica, T. leptophylla, T. madagascariensis*
	Group B.	*Tambourissa kirkii, T. paradoxa*
3.		*Tambourissa capuronii, T. moheliensis*
4.		*Tambourissa gracilis, T. purpurea, T. religiosa*
5.		*Tambourissa amplifolia, T. cocottensis, T. cordifolia, T. pedicellata, T. tau, T. tetragona*
6.		*Tambourissa bathiei, T. sieberi*
7.		*Tambourissa perrieri, T. quadrifida*
8.		*Tambourissa alaticarpa, T. longicarpa*
9.		*Tambourissa castri-delphinii, T. ficus, T. peltata*

Group 1. This is a group of Madagascan species with canescent to velutinous or tomentose stems, leaves, and inflorescences (Table 5). The inflorescence is usually a ramiflorous or axillary (rarely cauliflorous) pleiochasium, often sexually mixed and frequently terminated by a gynoecious flower, or the flowers may be solitary. Long acute, subulate or deltoid bracteoles subtend the pedicels and floral axis. The androecious flower splits open flat into 4(–5) segments, bears scattered hairs internally in many species, and has fairly numerous stamens, frequently with prolonged connectives. The urceolate, napiform or subglobose gynoecious flower opens by a small four-lobed, X-shaped orifice in most, and the densely velutinous internal surface is lined with many shortly conical styles. In most species, an abundance of oil cells occurs in the floral ground tissue of both sexes.

Group 1A. This group is comprised of three species with densely pubescent, usually apically toothed, adult leaves (*Tambourissa thouvenotii, T. trichophylla*) and densely velutinous-tomentose mature stems (Table 5). *Tambourissa uapacifolia* fits here on the basis of its dense pubescence, although its leaves are entire and the inflorescence is apparently unisexual.

Group 1B. Five species with entire leaves and sparsely pubescent to canescent adult leaves and stems comprise this group (Table 5): *Tambourissa decaryana, T. hildebrandtii, T. humbertii, T. nitida,* and *T. nosybensis.* Of these, *T. decaryana, T. humbertii,* and *T. nosybensis* show trends towards cauliflory and unisexual inflorescences.

Group 1C. The last group contains two species differing in having subglabrous mature growth and internally glabrous female flowers (Tables 5, 6). *Tambourissa floricostata* has few, large stamens and floral receptacles with longitudinal lateral ridges; it was formerly placed in *Schrameckia* (Danguy, 1928). In *T. parvifolia,* the leaves are small and sclerophyllous and the stamens slender with distinct filaments lacking prolonged connectives.

Group 2. This diverse group includes species from the Comores, Madagascar, and Réunion, some of which appear to be much more closely related than others (Tables 5, 6). Most have glabrous to sparsely pubescent mature growth and inflorescences. Varying degrees of reduction occur in the inflorescence, which ranges from a sexually mixed or unisexual pleiochasium to a fascicle or solitary flowers. Small deltoid bracteoles subtend the often long, slender floral axis and pedicels. Two subgroups can be distinguished.

Group 2A. This category consists of species with medium-sized to large, 4-fid androecious flowers that open flat and contain numerous long stamens with separate or apically confluent loculi and scarcely or non-prolonged connectives (Tables 6, 7). The gynoecious flowers are globose-depressed, closed in bud, internally ± glabrous with crowded, shortly columnar blunt styles, open by an X-shaped orifice, and produce a copious mucilaginous secretion in the two Réunion species (*Tambourissa crassa, T. elliptica*) and *T. beanjadensis* (Madagascar). In *T. madagascariensis* (Madagascar) and the Comorean species (*T. comorensis, T. leptophylla*) the orifice of the gynoecious receptacle is entire, internally pubescent and remains open during the entire floral development, a condition which is probably highly specialized (P. Endress, pers. comm.). Styles of the two latter species are bluntly columnar and shortly conical, respectively.

Group 2B. This group consists of two Comorean species in which the androecious flowers are small and globular, splitting only slightly and remaining nearly closed (*Tambourissa kirkii*), or merely opening by a small apical pore lined with scale-like tepals (*T. paradoxa*) (Table 6). In both species stamens are fewer, smaller, and more acute than in Subgroup A and have separate, medial loculi and acute, prolonged connectives. Androecious flowers of *T. moheliensis* correspond well with this group, but because its gynoecious flowers differ markedly from the other members, it will be discussed under Group 3. Gynoecious flowers of *T. kirkii* have an entire, circular orifice like *T. comorensis* and *T. leptophylla,* thus linking it to Group 2A; those of *T. paradoxa* are unknown.

Group 3. Members of this group are characterized by comparatively large, brown napiform gynoecious flowers that are closed and apically depressed in bud, later opening by a four-lobed, X-shaped orifice (Table 6). Unlike Group 2, the floral ground tissue contains numerous dark brown, presumably tanniferous, idioblasts. Androecious flowers of *Tambourissa capuronii* (Madagascar) are large, split open flat into four lobes, and have numerous large stamens with elongated lateral loculi. Those of *T. moheliensis* (Comores) are much smaller than in the former species, only split slightly open at anthesis (as in Group 2B), and differ in having fewer stamens with loculi that unite basally into a U-shape. Its androecious flowers therefore link Group 2B with Group 3.

Group 4. This group is composed of three Madagascan species which are glabrous to subglabrous, ramiflorous shrubs or small trees, mostly with arching branches, and have characteristic terminal dichasia, condensed pleiochasia or solitary flowers (Tables 5, 6). The gynoecious flowers and fruit are terminal, whereas the androecious flowers are either lateral, axillary, or ramiflorous. Floral receptacles are small and globose, monomorphic in both sexes, and open by small apical pores flanked by minute tepals. The comparatively small ripe fruiting receptacles are smooth and dark reddish externally, not pale and corky brown as in most other species. *Tambourissa gracilis* and *T. purpurea* both have similar androecious flowers with short, sessile stamens having apically confluent, crescentiform loculi; gynoecious flowers of the former are unknown. Flowers of *T. religiosa* are somewhat larger with longer, shortly conical styles. Also, its stamens have distinct filaments and separate loculi. Gynoecious flowers of *T. purpurea* produce a mucilaginous plug or "hyperstigma" which occludes the pore; it is not known if this phenomenon occurs in the other two species.

Group 5. This group of subglabrous to glabrous trees, treelets and shrubs includes the bulk of the Mauritian species (Tables 5, 6). *Tambourissa pedicellata* seems to be the least specialized member in view of its monoecy, variability of floral disposition and inflorescence structure, and particularly its monomorphic androecious and gynoecious flowers with shallowly subglobose to cupuliform receptacles, relatively few parts, shortly conical styles, and stamens with separate loculi and distinct filaments.

Other members of the group (*Tambourissa amplifolia, T. cocottensis, T. cordifolia, T. tau,* and *T. tetragona*) display variations on this theme with varying degrees of specialization in one or more features. Leaves of most species are moderately small, opposite and decussate, and have distinct petioles. Trends of specialization are towards macrophylly (*T. amplifolia, T. tau*), clustering of the leaves into pseudoverticils of two to four pairs (*T. tau*), winged stems (*T. tetragona*), and reduction in petiole length (*T. cordifolia, T. tau*). Modifications of the inflorescence tend towards reduction from pleiochasia to dichasia, and finally to fascicles and monochasia, towards a shortening of the pedicels and floral axis, and from ramiflory to (often basal) cauliflory.

Other apparent trends are towards greater floral dimorphism, towards larger flowers with more numerous parts (*T. cordifolia*), and towards staminal structural modifications such as fusion of the loculi apically (*T. amplifolia*), basally (*T. cordifolia*), or their extreme separation on lateral arms (*T. tau*). Gynoecious flowers display a greater deepening and closure (*T. cocottensis, T. tetragona*) or opening (*T. peltata*), modifications of the styles via elongation (*T. tau*) or shortening (*T. peltata*), and elaborate development of the receptacular lobes with bright coloration to enhance their attractive potential for pollinators (*T. cordifolia, T. peltata*). The latter two species are further specialized in being dioecious. Gynoecious flowers of *T. ficus* correspond to this group in spite of their gigantism. Because of the ternate leaves and androecious floral morphology, however, I have included *T. ficus* under Group 9.

Group 6. This group consists of two species of large, monoecious trees, i.e., *Tambourissa sieberi* (Mauritius) and *T. bathiei* (Madagascar).

Both have relatively small leaves, moderately to densely pubescent new growth and densely yellowish velutinous, cauliflorous inflorescences which are generally unisexual pleiochasia or thyrses (Tables 5, 6). The globose female receptacle opens by a small pore in *T. sieberi* (mature gynoecious flowers unknown in *T. bathiei*), and is lined with numerous long, narrowly conical, generally coalescent styles. Androecious flowers of both species are large and 4–5-fid with lobes that spread open flat and have numerous large stamens.

Group 7. Apparently related to Group 6, this category also contains two species not closely allied to other members of the genus: *Tambourissa quadrifida* (Mauritius) and *T. perrieri* (Madagascar). Both are glabrous cauliflorous trees with relatively small, opposite leaves, grow in relatively drier habitats, and produce numerous unisexual or sexually mixed pleiochasia or thyrses along most of the trunk (Tables 5, 6). Androecious flowers of both species split deeply into four flat or strongly recurved segments and bear hundreds of short stamens. The ellipsoid to obovoid or obpyriform gynoecious flowers open by a small, three- to four-lobed apical pore, are internally velutinous and contain hundreds of very short, basally ventricose styles. The mature fruiting receptacles of both are elongated with a small orifice, resembling those of Group 8.

Group 8. This isolated pair of Madagascan species, *Tambourissa alaticarpa* and *T. longicarpa*, formerly comprised the genus *Phanerogonocarpus*. Both are pubescent, monoecious, cauli- to ramiflorous treelets of the eastern wet forest zone with large, dentate leaves (Tables 5, 6). The pubescent, sexually mixed (rarely unisexual) inflorescence consists of one or two (rarely three) terminal gynoecious flowers with lateral clusters of relatively small androecious flowers grouped along the floral axis, a feature shared with certain members of Groups 1 and 7. The stamens have distinct filaments, free loculi, and the connective may or may not be prolonged. Most distinctive of Group 8 are the slender, obovoid to cylindrical, narrowly ribbed or winged gynoecious flowering and fruiting receptacles with a small orifice. Gynoecious receptacles of *T. floricostata* (Group 1C) are also ribbed, however, and those of Group 7 are ellipsoid to obovoid, although not as narrow, with comparably small orifices. The conical to ventricose styles are interspersed with dense short hairs in both species, and a mucilaginous exudate is apparently produced in *T. longicarpa*.

Group 9. Characterized by ternate to subalternate adult leaves with prominent, highly organized and finely reticulate venation, this group consists of three species (Tables 5, 6), i.e., *Tambourissa castri-delphinii* (Madagascar), *T. ficus*, and *T. peltata* (both Mauritius). Flowers are produced either at the base of the trunk (*T. ficus*), or on the upper trunk and older branches (*T. peltata* and *T. castri-delphinii*). The highly reduced inflorescence ranges from a short, condensed pleiochasium or fascicle in the latter, to a two-flowered fascicle or monochasium in the other two species. The group also displays a trend towards dioecy.

Androecious flowers of *Tambourissa ficus* are the largest in the entire genus, with five to seven incurved or spreading lobes bearing from 900 to 1,800 ligulate stamens with separate, lateral to unifacial loculi and a thick, prolonged connective. Androecious flowers of *T. peltata* and *T. castri-delphinii* are considerably smaller, deeply split into four or five recurved lobes, and bear numerous thin, broadly deltoid subsessile stamens with connivent or confluent lateral loculi.

Gynoecious flowers of *Tambourissa peltata* are highly specialized, flat and discoid with four to seven elaborate, spreading verrucose sterile lobes and numerous crowded, highly reduced, flat columnar styles which produce a copious mucilaginous exudate. Those of *T. castri-delphinii* have an X-shaped orifice and conical styles, similar to some species in Group 5. In *T. ficus* the gynoecious flowers are huge and urceolate, splitting into numerous straight or inflexed lobes with a broad orifice, and contain ca. 1,000–2,000 setose styles. Apart from their great size, gynoecious flowers of *T. ficus* are morphologically similar to those of species belonging to Group 5 and link the two groups.

In the following key I have attempted to utilize vegetative characters as far as possible. Although certain species with outstanding vegetative characters are identifiable even from sterile specimens (e.g., *Tambourissa tetragona* is the only species with winged stems), for the majority, complete collections consisting of leafy stems, androecious and gynoecious flowers, and fruits are essential for reliable identification. Unfortunately, a large number of species, especially those from Madagascar and the Comores, are known only from androecious or gynoecious flowers or fruits, and this has imposed certain limitations on the construction of this key. Although I was unable to examine all the Madagascan material cited by Cavaco (1959), I have seen additional material not cited by him. All collections in the Exsiccata and virtually all those used to plot the distribution maps have been seen by me. The last five species in the taxonomic treatment (nos. 39–44) are imperfectly known and consequently have not been included in the key. See key cited on following pages.

1. **Tambourissa trichophylla** Baker, J. Linn Soc., Bot. 20: 240. 1884; Perk. & Gilg, Pflanzenr. 4, 101: 68. 1901; Drake in Grandidier, Hist. Phys. Madagascar 1(1): 24. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 41. 1911; Cavaco in Humbert, Fl. Madagascar 80: 24, fig. VII:8–9. 1959. TYPE: Madagascar. ("Central Madagascar," probably Tananarive or Fianarantsoa): without precise locality, 1882 (fl), *Baron 1953* (lectotype, K, here designated).

Monoecious treelet or tree attaining 15 m tall and 15–20 cm D.B.H., the new growth densely pilose-tomentose, the hairs simple, pale yellowish to grayish, the mature leafy stems 2–4 mm diam., tomentose, the hairs ± matted. Leaves opposite to subopposite, petiolate; petioles tomentose, 4–10 mm by 1.5–2 mm; lamina chartaceous to subcoriaceous, oblong, narrowly oblong, narrowly obovate, lanceolate or rarely elliptic, (50–)70–195 mm by 20–52 mm, the apex shortly acuminate, shortly acute or rarely obtuse, the base obtuse to rounded, rarely acute, abaxially tomentose-hirsute, especially along costa and secondary veins, the trichomes curved, adaxially pilose when young, glabrescent, the secondary veins 3–5 pairs, making a 50–60° angle with the costa, the arches low and broad, the venation disorganized, obscure adaxially and visible to 2°, prominent abaxially and visible to 3°, the margin slightly thickened and revolute, ciliate, entire or usually serrate-dentate in the apical ⅓–¼ of the lamina with 1–2 pairs of short, broadly deltoid teeth. Inflorescence ramiflorous on leafless nodes or axillary, a usually unisexual, sometimes leafy pleiochasium of 3–7 flowers, or the flowers solitary, the floral axis fulvous to grayish, velutinous-tomentose, 14–55 mm by 1.5–2 mm, subtended by several deltoid-naviculate bracteoles 1–2 mm long, the pedicels 3–5 mm by 1.5 mm, each subtended by 1(–2) subulate velutinous bracteoles 4–5 mm long. Androecious flower in bud globose, 5–7 mm diam., hirsute, apiculate with several pairs of minute hirsute tepals; androecious flower at anthesis unknown (presumably deeply 4-fid with spreading lobes as in *T. thouvenotii*); stamens in bud ca. 100, ovoid-deltoid, 1.5–2 mm long by 0.8–1 mm wide, the loculi lateral, separate, occupying ca. ¾ total length of stamen, the filament short or sessile, the connective thick, slightly prolonged apically, the internal receptacle surface with clusters of hairs between the stamens. Gynoecious flower in bud solitary or occasionally in pleiochasia, 7–8 mm diam. by 5–6 mm long, subglobose-depressed, hirsute, apiculate with 4 minute deltoid tepals; at anthesis shallowly 4(–5)-fid, the lobes ± incurved, the small X-shaped orifice 2–3 mm diam., the styles ca. 100, conical, 0.6–0.8 mm long by 0.3–0.4 mm wide basally, ± ventricose, acuminate, the internal receptacle surface velutinous between the styles. Fruiting receptacle solitary on the smaller branches, shallowly cupuliform, 30–48 mm diam. by 30 mm long, the walls 13–15 mm thick, both surfaces pale corky brown, the orifice subentire, comprising ca. ½ total diam. of the fruit, the scattered styles conical, 0.3–0.5 mm long and wide basally, the internal receptacle surface hirsutulous; pedicel and peduncle stout, 6–8 mm long by 7–12 mm diam., hirsutulous. Submature carpels 6–8 mm long, 4–5 mm wide, 3–4 mm thick, ovoid-compressed, the endocarp brown.

Distribution. Endemic to Madagascar (Fig. 27).

Habitat. The species is locally common and fairly widespread in the *Tambourissa/Weinmannia* wet forest zone in the eastern and central regions ranging from 800 to 1,500 m.

MADAGASCAR. TAMATAVE: Ankaraoka, ca. 1,500 m, 28 Dec. 1944 (fl, fr), *Anon. sub Herb. Alaotra 3073* (MAD); National Route no. 2 at 69 km E of Tananarive, Mandraka forest reserve, 1,400 m, 28 Oct. 1978 (fl), *Lorence 1879* (MAD, MAU, MO); 30 Oct. 1978 (fl), *Lorence 2034* (MAD, MO); (fl), *Lorence 2035* (MAD, MO); La Mandraka, Sept. 1963 (st), *Morat 7* (MAD); National Route no. 2 at ca. 20 km W of Perinet, 950 m, 29 Oct. 1978 (st), *Lorence 2000* (MAD, MO). TANANARIVE: Andringitra Massif, Ambodigraiss Forest near Antsirabe (sic), 1,200 m, 12 Jan. 1945 (fr), *Anon. sub Herb. Alaotra 2242* (MAD). PROVINCE UNCERTAIN: head of Ankafinka Valley, 16 Nov. 1965 (fr), *Rakotozafy 266* (MAD). WITHOUT PRECISE LOCALITY: Central Madagascar, 1882 (fl), *Baron 1975a*

KEY TO THE SPECIES OF *TAMBOURISSA*

[N.B.: for Madagascan material also refer to descriptions of last four species (nos. 39–43), not included in this key].

1a. **Mature leaves, petioles, and stems conspicuously pubescent (canescent, villous, or velutinous-tomentose).**
  2a. Gynoecious floral and fruiting receptacles narrowly obovoid-cylindrical, tubular, bearing 4–6 longitudinal ridges or narrow wings; Madagascar.
    3a. Leaves serrate-dentate with 9–10 pairs of narrow, acute teeth in apical ⅔ of lamina; staminal connective not prolonged beyond anther; gynoecious flower at most puberulent, glabrescent .... 34. *T. alaticarpa*
    3b. Leaves strongly dentate with (1–)2–3 pairs of broad, deltoid teeth in apical ⅓ of lamina; staminal connective prolonged beyond anther; gynoecious flower densely pubescent .... 35. *T. longicarpa*
  2b. Gynoecious floral and fruiting receptacles subglobose to cupuliform, at most ellipsoid to obovoid or pyriform, unwinged (if bearing 2 or many low, rounded ribs, then receptacle globose or discoid); Madagascar, Mascarenes, Comores.
    4a. Inflorescence a robust, cauliflorous, velutinous thyrse with 16–90 flowers; floral axis stout, 50–110 mm long; mature buds globose, 12–14 mm diam.; large tree, Mauritius .... 30. *T. sieberi*
    4b. Inflorescence and buds much smaller and sparser, a cauliflorous or ramiflorous pleiochasium; large or small trees; Madagascar.
      5a. Mature leaves abaxially velutinous-tomentose, at least on margins, costa and major veins; leafy stems and petioles velutinous-tomentose.
        6a. Adult leaves entire, the apex obtuse to retuse; loculi of stamens bearing scattered hairs externally, the connective not prolonged .... 3. *T. uapacifolia*
        6b. Adult leaves with 1–8 pairs of teeth in apical half of lamina, the apex shortly acute to acuminate, rarely obtuse; loculi of stamens glabrous, the connective prolonged.
          7a. Lamina elliptic to broadly elliptic, 50–90 mm wide; arches of secondary veins high and narrow; petioles 10–20 mm long; floral pedicels 12–17 mm long; fruit distinctly pedicellate .... 2. *T. thouvenotii*
          7b. Lamina narrowly oblong to oblong or oblanceolate, 20–50 mm wide; arches of secondary veins low, broad; petioles 4–10 mm long; floral pedicels 3–5 mm long; fruit subsessile to sessile .... 1. *T. trichophylla*
      5b. Mature leaves at most puberulent abaxially; stems and petioles canescent to sparsely villous.
        8a. Lamina very lustrous adaxially, dull abaxially, the apex long acuminate .... 4. *T. nitida*
        8b. Lamina dull on both surfaces, the apex at most acuminate.
          9a. **Apex of lamina very shortly acuminate to obtuse or retuse; gynoecious receptacle subglobose-napiform, not ribbed, the styles 1–1.5 mm long, strongly papillose in both flower and fruit; stamens with a very short, apiculate connective** .... 5. *T. hildebrandtii*
          9b. **Apex of lamina acuminate; gynoecious receptacle discoid, ribbed, the styles 0.4–0.6 mm long, not papillose; stamens with an acute, prolonged connective 0.5 mm long** .... 6. *T. nosybensis*

1b. **Mature leaves, petioles, and stems glabrous, or at most with rare, scattered hairs.**
  10a. Adult leaves ternate, dissociate or even subalternate, except rarely opposite in *T. castri-delphinii.*
    11a. Flowers in short pleiochasia or fascicles of (3–)4–9 flowers on a common axis, never solitary, the pedicels slender, 0.5–1 mm diam.; Madagascar, E coast, Manakara to Fort Dauphin .... 36. *T. castri-delphinii*
    11b. Flowers solitary or in pairs, never on a common axis, the pedicels stout, 1.5–4.5 mm diam.; Mauritius.

12a. Buds, pedicels, and new vegetative growth puberulent; inflorescence basally cauliflorous; stamens 900–1,800, 0.5–1 mm wide, the loculi separate, the thick, obtuse connective prolonged for ¼–⅓ total length of stamen; gynoecious flower massive, urceolate, with 6–8 erect to incurved lobes, the styles 1,000–2,000, setose, 1.5–5 mm long .... 37. *T. ficus*

12b. Buds, pedicels, and new vegetative growth glabrous; inflorescence ramiflorous, rarely cauliflorous on top part of trunk; stamens 200–400, 1.5–3 mm wide, the loculi confluent apically or the connective only slightly prolonged; gynoecious flower flat and discoid with 4–7 broad, spreading-reflexed lobes, the styles 400–500, crowded, columnar, flat-topped, coalescent, 0.5 mm long .... 38. *T. peltata*

10b. Adult leaves strictly in decussate pairs, opposite or rarely subopposite.

13a. Leafy stems quadrangular, conspicuously winged; Mauritius, summit of Mt. Cocotte .... 27. *T. tetragona*

13b. Leafy stems terete or subterete, neither quadrangular nor winged.

14a. Leaf base strongly cordate and amplexicaul; dioecious shrubs 50–150 cm high; Mauritius, in *Philippia* heath formation or low scrub .... 29. *T. cordifolia*

14b. Leaf base acute to weakly cordate, not amplexicaul; larger treelets or trees; forests of Mauritius, Réunion, Madagascar, Comores.

15a. Leaves pseudoverticillate, clustered in 2–4 pairs separated by long intervals.

16a. Stamens ± T-shaped with separate loculi; buds and flowers externally corky brown; styles setose, 2–3 mm long; orifice of gynoecious flower with 5–10 irregular incurved deltoid lobes .... 26. *T. tau*

16b. Stamens clavate with apically confluent loculi; buds and flowers not externally corky; styles shortly conical, 0.6–1 mm long; lobes of female receptacle 4, deltoid, ± erect .... 25. *T. amplifolia*

15b. Leaves regularly disposed in pairs along stem.

17a. Mature inflorescence externally glabrous (or corky), at most with rare scattered hairs, not conspicuously nor finely pubescent under dissecting microscope.

18a. Flowers large, solitary, and terminal on branches (rarely terminal on leafy cauliflorous shoots); buds and female receptacles 12–15 mm diam.; androecious flowers splitting into 4–5 lobes, opening to 40–50 mm diam.; dioecious trees or treelets; leaves large, thick, obtuse to retuse, the higher order venation (3° and above) obscure, when dry fragrant and often bright yellow-green; Réunion .... 14. *T. crassa*

18b. Flowers in dichasia or pleiochasia, rarely solitary or in fascicles of 2, either ramiflorous, axillary or terminal (if solitary, then buds and flowers much smaller, less than 9 mm diam.); leaves smaller and thinner, when dry not fragrant, dull dark green or brownish, not bright yellow-green; Mauritius, Réunion, Madagascar, Comores.

19a. Floral pedicel and peduncle acutely quadrangular, 5–7 mm long, bearing four rows of decussate ciliate bracteoles; buds and flowers externally corky brown, cauliflorous, solitary or in groups of 2; Mauritius, summit of Mt. Cocotte .... 28. *T. cocottensis*

19b. Floral pedicel and peduncle terete to subtetragonal, neither quadrangular nor with four rows of bracteoles; Mauritius, Madagascar, Réunion, Comores.

20a. Adult leaves small, coriaceous, 15–45 mm by 9–22 mm, obovate, elliptic or oblong, the apex obtuse to retuse; inflorescence ramiflorous on leafless stems, a lax, glabrous to canescent pleiochasium ca. 25–70 mm long; small monoecious trees; montane forests, central Madagascar .... 10. *T. parvifolia*

20b. Adult leaves mostly much larger, the inflorescence mostly exceeding 15 mm long; if leaves as small, then inflorescence axillary or terminal on leafy stems, a short, congested dichasium or pleiochasium 10–15 mm long, or the flowers rarely solitary; Madagascar, Mauritius, Réunion, Comores.

21a. Inflorescence and buds externally corky and pale brown; androecious buds 15–19 mm diam.; connectives of stamens acute, prolonged, with several hairs at apex; Madagascar .... 20. *T. capuronii*

21b. Inflorescence and buds externally smooth, dark brown or blackish, never corky; androecious buds 2–11 mm diam.; connectives of stamens prolonged or lacking, but never bearing hairs; Madagascar, Mauritius, Réunion, Comores.

22a. Inflorescence terminal or axillary, a short, congested dichasium or pleiochasium 10–15 mm long (flowers rarely solitary); Madagascar.

23a. Leaves larger, 70–150 mm by 30–60 mm; lamina coriaceous, the 3–5° veins prominent abaxially, a marginal fimbrial vein present; buds and flowers 7–10 mm diam. by 4–7 mm long; stamens 60–82, with distinct filament and separate loculi .... 21. *T. religiosa*

23b. Leaves usually much smaller, 40–85 mm by 15–40 mm; lamina subcoriaceous, the 3–4° veins not prominent, a marginal fimbrial vein absent; buds and flowers 3–5.5(–7) mm diam. by 2.5–6(–7) mm long; stamens 20–32, ± sessile, the filament not distinct, the loculi confluent apically into a single crescentiform loculus .... 22. *T. purpurea*

22b. Inflorescence rami- or cauliflorous, a lax, occasionally leafy, pleiochasium or thyrse greatly exceeding 15 mm long (flowers occasionally solitary, axillary); Mauritius, Réunion, Comores, Madagascar.

24a. Androecious receptacle splitting for less than half its length into 4–5 short, incurved or erect lobes, or opening by a small, subentire apical pore.

25a. Floral pedicels 15–66 mm long, glabrous; androecious receptacle shallowly 4–6-fid, the lobes lacking scale-like tepals internally; stamens with separate loculi; leaf apex shortly acuminate, acute, obtuse or retuse; Mauritius .... 24. *T. pedicellata*

25b. Floral pedicel 5–13 mm long, with scattered hairs; androecious receptacle with obtuse, scale-like tepals internally on the lobes or flanking the orifice; stamens with confluent loculi; leaf apex acute to long acuminate.

26a. Androecious flowers opening by a small, circular orifice 1–2 mm diam.; stamens ± sessile with apically confluent loculi; leaf apex acuminate; Madagascar .... 23. *T. gracilis*

26b. Androecious flower splitting into 4 shallow lobes; stamens with loculi confluent basally into a U-shape; leaf apex acute or rounded; Mohéli (Comores) .... 19. *T. moheliensis*

24b. **Androecious receptacle deeply split at anthesis for more than half its length into (3–)4–5 deltoid lobes that ultimately spread open flat or reflex.**

  27a. **Gynoecious receptacle longer than wide, obovoid to pyriform or ellipsoid;** cauliflorous species; inflorescence a stout pleiochasium or thyrse 60–180 mm long; floral axis 2–4 mm diam.

    28a. Leaves thin, chartaceous, slightly lustrous, the ultimate venation prominent and raised on both surfaces, the apex acuminate; orifice of gynoecious flower 3–4 mm diam. (ca. ½ total width of receptacle); androecious buds globose; Madagascar .... 32. *T. perrieri*

    28b. Leaves subcoriaceous, dull, the ultimate venation frequently obscure on both surfaces, the apex shortly acuminate to mucronate, obtuse, rounded or retuse; orifice of gynoecious flower 1–2 mm diam. (ca. ¼ total width of receptacle); androecious buds obovoid to ellipsoid; Mauritius, dry western forests .... 33. *T. quadrifida*

  27b. **Gynoecious receptacle as wide as or wider than long, subglobose to globose-depressed or napiform-depressed; ramiflorous species; inflorescence a slender pleiochasium 20–50 mm long; floral axis 1–1.5 mm diam.** (if cauliflorous, then flowers solitary or in fascicles of 2–3).

    29a. Floral axis 20–45 mm long; androecious buds distinctly apiculate; Madagascar.

      30a. Lamina 34–47 mm by 18–28 mm; stamens 35–36, sessile, obtuse to deltoid, 0.6–1 mm long, the loculi apically confluent into a single crescentiform loculus; orifice of gynoecious flower closed in bud, at anthesis 4-lobed, X-shaped .... 11. *T. beanjadensis*

      30b. Lamina 42–80 mm by 24–34 mm; stamens ca. 200, lanceolate to subulate, 2.5–4 mm long, the loculi separate, lateral; orifice of gynoecious flower open in bud, at anthesis circular, entire .... 12. *T. madagascariensis*

    29b. Floral axis 10–15 mm long (or in the flowers solitary); androecious buds not markedly apiculate; Réunion .... 13. *T. elliptica*

17b. Mature inflorescence canescent to velutinous-tomentose or strigillose with conspicuous, often fine and ± appressed hairs under dissecting microscope.

  31a. Leaves highly lustrous adaxially, dull abaxially; Madagascar .... 4. *T. nitida*

  31b. Leaves not markedly lustrous adaxially, dull on both surfaces; Madagascar, Mauritius, or Comores.

    32a. Lamina macrophyllous, ca. 150–325 mm by 85–115 mm; gynoecious flowers in pleiochasia of 6–11, the pedicels 6–23 mm long, the receptacle napiform-depressed, 7–8 mm diam. by 4–5 mm long, the orifice X-shaped, 4(–5)-lobed, the lobes incurved with inner surface bearing 25–40 sterile appendages resembling styles but larger (androecious flowers unknown); Madagascar .... 7. *T. decaryana*

    32b. Leaves smaller, or if as large then floral pedicels 25–60 mm long; female receptacle lobes lacking **conspicuous style-like sterile appendages on inner surface (or gynoecious flowers unknown); Madagascar, Mascarenes, Comores.**

33a. Androecious and gynoecious floral receptacles with 2–4 low, external longitudinal ridges .... 9. *T. floricostata*

33b. Androecious and gynoecious floral receptacles lacking 2–4 external ridges (numerous low ribs present in gynoecious flowers of *T. nosybensis*).

- 34a. Styles bearing long (1–1.5 mm), scattered hairs externally; gynoecious buds and flowers 15–20 mm diam.; Madagascar .... 8. *T. humbertii*
- 34b. Styles glabrous or, if bearing scattered hairs, these much shorter, 0.5 mm long (in *T. kirkii,* Anjouan); gynoecious buds and flowers 7–15(–16) mm diam.; Mauritius, Madagascar, Comores.
  - 35a. Androecious receptacle remaining partly or almost completely closed at anthesis, either shallowly split or globose with subentire apical pore; stamens narrowly acute, tapering gradually to a slender, conspicuously prolonged connective; Comores.
    - 36a. Androecious receptacle opening by a small apical orifice ca. 2 mm diam. flanked internally by several series of small, obtuse scale-like tepals; prolonged connectives slightly exserted from orifice; gynoecious flowers unknown; Anjouan. .... 18. *T. paradoxa*
    - 36b. Androecious receptacle splitting into 3–4 shallow segments, lacking small, obtuse scale-like tepals internally; tips of staminal connectives not exserted from orifice; Anjouan, Mohéli.
      - 37a. Staminal loculi separate; orifice of gynoecious receptacle circular, entire; Anjouan .... 17. *T. kirkii*
      - 37b. Staminal loculi mostly united basally into a U-shape; orifice of gynoecious receptacle with 4 large deltoid lobes; Mohéli .... 19. *T. moheliensis*
  - 35b. Androecious receptacle splitting more than halfway open, the lobes spreading flat or reflexing at anthesis, the staminal connectives only slightly or not prolonged (except in *T. moheliensis*); Mauritius, Madagascar, Comores.
    - 38a. Mature floral pedicels 25–80 mm long.
      - 39a. Lamina 250–430 mm by 80–230 mm; flowers either solitary, fasciculate, or in short pleiochasia of 3–7; androecious flowers at anthesis 14–18 mm diam.; stamens 1–1.5 mm long, the loculi apically confluent; slender, basally cauliflorous treelets; Mauritius .... 25. *T. amplifolia*
      - 39b. Lamina generally much smaller; flowers in ample pleiochasia or thyrses of 7–34; androecious flowers at anthesis 20–35 mm diam.; stamens 2–3 mm long, the loculi separate (apically confluent in *T. bathiei,* Madagascar); larger trees; Madagascar, Comores.
        - 40a. Orifice of gynoecious floral receptacle circular, entire, open even in bud; androecious buds 6–8 mm diam.; Mayotte (Comores) .... 16. *T. leptophylla*
        - 40b. Orifice of gynoecious floral receptacle closed in bud, at anthesis splitting into a 4-lobed, X-shaped orifice with deltoid lobes; Comores, Madagascar.

41a. Gynoecious buds and flowers externally corky brown, napiform, the apex strongly depressed; lamina 120–220 mm by 40–70 mm; Mohéli (Comores) .... 19. *T. moheliensis*

41b. Gynoecious buds and flowers externally fulvous velutinous-canescent, globose, the apex apiculate; lamina 40–58 mm by 20–25 mm; Madagascar .... 31. *T. bathiei*

38b. Mature floral pedicels 5–15 mm long.

42a. Leaves small, 14–45 mm by 9–22 mm, coriaceous, obovate, elliptic or oblong, the apex obtuse to retuse; inflorescence puberulent or sparsely canescent; montane forests of central Madagascar .... 10. *T. parvifolia*

42b. Leaves much larger, generally exceeding 50 mm long, if apex retuse or obtuse, then inflorescence villous-tomentose; Madagascar, Comores.

43a. Gynoecious receptacle open even in bud, the orifice circular and entire; Comores.

44a. New stems and leaves glabrous; inflorescence a short pleiochasium of 4–9 flowers; mature androecious buds 9–14 mm diam.; stamens 125–150; gynoecious flowers and fruit with short, bluntly columnar styles ca. 0.5 mm long; gynoecious floral orifice ca. ½–⅔ total diam. of receptacle; fruit smooth, mottled reddish brown, the orifice ca. ⅓–½ total diam. of receptacle; Grande Comore .... 15. *T. comorensis*

44b. New stems and leaves finely pubescent; inflorescence a lax pleiochasium or thyrse of (5–)7–25 flowers; mature androecious buds 6–8 mm diam.; stamens ca. 80–90; gynoecious flowers and fruit with sharply acute, conical styles ca. 0.6–1 mm long; gynoecious floral orifice ca. ¼–⅓ total diam. of receptacle; fruit uniformly dull, corky brown, the orifice ca. ⅙–¼ total diam. of receptacle; Mayotte .... 16. *T. leptophylla*

43b. Gynoecious receptacle closed in bud, at anthesis splitting into 4 shallow lobes, the orifice X-shaped; Madagascar.

45a. Apex of lamina shortly acuminate to obtuse or retuse; gynoecious receptacle subglobose to napiform, not ribbed externally, the styles 1–1.5 mm long, strongly papillose in flower and fruit; stamens with a very short, apiculate connective; Madagascar .... 5. *T. hildebrandtii*

45b. Apex of lamina long acuminate; gynoecious receptacle discoid, externally many-ribbed, the styles ca. 0.4–0.6 mm long, not papillose; stamens with an acute, prolonged connective ca. 0.5 mm long; Nosy-Be island (NW Madagascar) .... 6. *T. nosybensis*

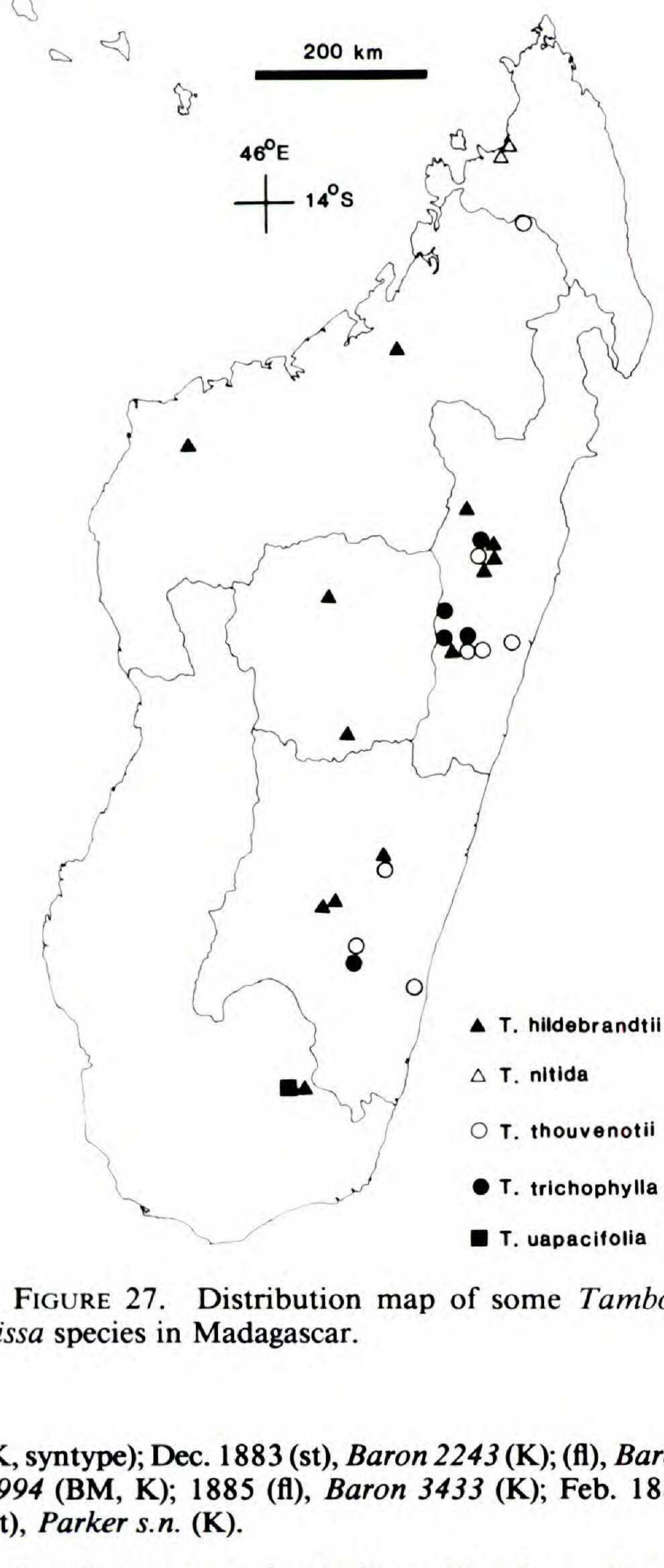

FIGURE 27. Distribution map of some *Tambourissa* species in Madagascar.

(K, syntype); Dec. 1883 (st), *Baron 2243* (K); (fl), *Baron 2994* (BM, K); 1885 (fl), *Baron 3433* (K); Feb. 1882 (st), *Parker s.n.* (K).

Tambourissa trichophylla and its close ally, *T. thouvenotii*, are both characterized by apically dentate adult leaves. This character may represent a state of neoteny, as it occurs in young plants and sucker shoots of many other *Tambourissa* species. *Tambourissa trichophylla* is distinguishable from *T. thouvenotii* by its narrower oblong leaves with fewer and broader teeth (only 1–3 pairs), its more widely spaced secondary veins with lower, stronger arches, its sparser and more curved trichomes, and its smaller flowers with much shorter pedicels and longer bracteoles. Both species remain distinct where they occur sympatrically and both belong to species Group 1A.

Vernacular name. Ambora saha (Madagascar).

2. **Tambourissa thouvenotii** Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 28: 250. 1922. TYPE: Madagascar. Tamatave: Analamazaotra (Perinet), ca. 1919 (fl), *Thouvenot 109* (lectotype, K, here designated; isolectotypes, P, 2 sheets).

T. trichophylla Baker var. *thouvenotii* Cavaco in Humbert, Fl. Madagascar 80: 25, fig. VII:1–4. 1959.

Monoecious or subdioecious treelet or tree 8–22 m tall and 15 cm or more D.B.H., the new growth densely velutinous, the trichomes simple, yellowish, the mature leafy stems velutinous, 3–5 mm diam. (sucker stems to 12 mm diam.). Leaves opposite, petiolate; petioles velutinous, 10–20 mm by 2–3 mm; lamina subcoriaceous, broadly elliptic to elliptic, rarely broadly oblong, ovate or obovate, (70–)85–185 mm by (37–)50–90 mm, the apex shortly acuminate, rarely obtuse, the base obtuse to rounded, the young lamina adaxially pilose, glabrescent except on costa and major veins, abaxially densely velutinous with soft, straight yellowish hairs, the secondary veins 4–7 pairs, making a 35–50° angle with the costa, the arches high and narrow, the venation obscure adaxially and visible to 2°, prominent abaxially and visible to 4°, the margin slightly thickened and revolute, ciliate, the apical ⅓–⅔ of the lamina usually serrate-dentate with 1–8 pairs of short teeth. Inflorescence cauliflorous, ramiflorous or axillary, a sexually mixed or unisexual pleiochasium of 3–7 flowers, or the flowers rarely solitary, the floral axis velutinous, 25–57 mm by 2–3 mm, subtended by several velutinous, deltoid-subulate bracteoles 2–3 mm long. Androecious flower in bud globose, 10–12 mm diam., hirsute-velutinous, apiculate with several minute, velutinous tepals, the pedicel 12–17 mm by 1.5–2 mm; at anthesis deeply 4-fid, 12–25 mm diam., the lobes spreading flat; stamens numerous, ca. 50–100, deltoid-lanceolate to subulate, 3–7 mm long by 1–1.5 mm wide, slightly incurved, the filament short or sessile, the loculi lateral to slightly unilateral, separate, occupying ⅔–¾ total length of the stamen, the connective prolonged apically, acute, the internal receptacle surface pubescent. Gynoecious flower in bud broadly napiform-depressed, 11–13 mm diam. by 6–7 mm long, velutinous, apiculate with several minute tepals, the pedicel 6–10 mm long; at anthesis shallowly and irregularly 5–6-lobed, the orifice 3–4 mm diam., the lobes incurved, not reflexed; styles numerous, ca. 100–150, very shortly conical, 0.3 mm long by 0.2 mm wide basally, the apex acuminate to acute, the internal receptacle surface velutinous between the styles. Fruiting receptacle solitary on old branches, irregularly cupuliform, 40–100 mm diam. by 32–55 mm long, the walls 12–18 mm thick, both surfaces corky, reddish brown, externally hirsute-velutinous, the orifice subentire, comprising ¼–½ total width of the fruit; styles numerous, shortly conical, 0.3–1.6 mm long by 0.3–0.5 mm wide basally; pedicel and peduncle 15–50 mm long by 9–15 mm wide. Mature carpels 15–16 mm long, 6–7 mm wide, 4–5 mm thick, the endocarp light brown, the surface scrobiculate.

Distribution. Endemic to Madagascar (Fig. 27).

Habitat. *Tambourissa thouvenotii* is fairly widespread and often locally common in the *Tambourissa/Weinmannia* montane wet forest zone of the eastern and central regions from ca. 800 to 1,400 m. In addition to the obvious morphological differences, both *T. thouvenotii* and *T. trichophylla* appear to occur sympatrically in at least some areas, e.g., Massif d'Andringitra (*Anon. sub Herb. Alaotra 2242,* MAD; *Anon. sub Herb. Alaotra 2311,* MAD), where they remain distinct.

MADAGASCAR. MAJUNGA: Circagri Bealanana (near Tsaratanana massif), June 1953 (st), *Anon. sub Agronomic Service s.n.* (MAD). FIANARANTSOA: Ampamherana, Fianarantsoa, 24 Nov. 1949 (fl), *Anon. sub SF 1248* (MAD); Andringitra Massif, Ambatapaiso near Antsirabe (sic), 12 Jan. 1945 (st), *Anon. sub Herb. Alaotra 2311* (MAD); in rain forest, Tsararano, Vondrozo district (E coast, near Farfangana), Dec. 1963 (fl), *Bosser 18583* (MAD). TAMATAVE: Ranomafana East, 300–400 m (fr), *Chebonis s.n.* (MAD); Analamazaotra Forest (near Perinet), Jan. 1919 (fl), *Anon. sub SF 73* (probably a syntype, MAD); National Route no. 2 at 1 km W of Perinet, ca. 900 m, 29 Oct. 1978 (st), *Lorence 2014* (MAD, MAU, MO); (st), *Lorence 2015* (MAD, MAU, MO); Perinet, 950 m, 13 Aug. 1968 (st), *McWhirter 121* (K); Analamazaotra, (fl), *Thouvenot 73* (K, P, syntypes); 1919 (fl), *Thouvenot s.n.* (BM); Andovoranto Province, Moramanga District, Analamazaotra Forest, 950 m, 3 Nov. 1912 (st), *Viguier & Humbert 1106* (G); Ambatondrazaka (fl), *Anon. sub SF 2548* (MAD). WITHOUT PRECISE LOCALITY: North Madagascar, 1892 (fr), *Baron 6721* (K).

Tambourissa thouvenotii seems most closely related to *T. trichophylla,* which also possesses dentate-serrate adult leaves. It is distinguishable from the latter species by its much larger, broader and usually elliptic leaves with more numerous teeth (up to 8 pairs) and more closely spaced secondary veins with higher and weaker arches showing a tendency to become almost craspedodromous (Fig. 7A). *Tambourissa thouvenotii* also has a denser, more yellowish indument of straight hairs, much longer floral pedicels, shorter bracteoles, and larger flowers than does *T. trichophylla.* Both species are closely allied to *T. uapacifolia* which also belongs to species Group 1A.

Vernacular names. Ambora, Ambora beravina (Madagascar).

3. **Tambourissa uapacifolia** Cavaco, Bull. Mus. Hist. Nat. (Paris), Ser. 2, 29: 351. 1957; Cavaco in Humbert, Fl. Madagascar 80: 24, fig. V:6–7. 1959. TYPE: Madagascar. Tulear: upper basin of the Mandrare River (SE), pass and summit of Marosoui, 1,000–1,400 m, 14–15 Nov. 1928 (fl, fr), *Humbert 6604* (holotype, P; isotypes, P, 2 sheets).

Monoecious tree, the new growth densely velutinous, the mature leafy stems 4–5 mm diam., velutinous-hirsute. Leaves opposite to subopposite, petiolate; petioles 5–16 mm by 1.5–2.5 mm, velutinous; lamina subcoriaceous, obovate to elliptic, 65–155 mm by 20–85 mm, hirsutulous when young, later glabrescent except abaxially on the major veins and margin, the apex obtuse or rarely shortly acute, the base acutely cuneate, rarely obtuse, the secondary veins 4–6 pairs, making a 40–50° angle with the costa, the venation depressed and visible to 3° adaxially, raised and visible to 4° abaxially, the margin thickened, slightly revolute, ciliate. Inflorescence cauliflorous or ramiflorous on leafless nodes, a velutinous, pendulous unisexual (always?) pleiochasium of 5–9 flowers, the floral axis 20–55 mm by 1.5–2 mm, subtended by small, naviculate bracteoles 1.5–2 mm long. Androecious flower in bud globose, 6–10 mm diam., velutinous, apiculate, the apex with several pairs of small, hirtellous-velutinous tepals, the pedicel velutinous, 10–17 mm by 1–1.5 mm; at anthesis 4-fid; 17–20 mm diam., stamens ca. 100–300, clavate, 1–2 mm long by 0.6–1 mm wide, the filament comprising ca. ⅓–½ the total length, the loculi lateral, separate or confluent apically, ± parallel, comprising ca. ½–⅔ total length of the stamen, the connective not prolonged, the external surface of loculi bearing medially several scattered simple hairs, the internal receptacle surface bearing scattered simple hairs between the stamens. Gynoecious flower unknown. Fruiting receptacle solitary on older leafless stems, the submature fruit cupuliform, 35–41 mm diam. by 20–27 mm long, the orifice ca. 10–15 mm diam., subentire, the walls 14–16 mm thick, externally pale corky brown with scattered hairs, the internal surface hirsute, the styles scattered, broadly conical, 0.5–0.6 mm long by 0.6–0.8 mm wide basally; pedicel and peduncle hirsute-velutinous, 25–50 mm long by 3–4 mm diam.; submature carpels 9–12 mm long, 7–8 mm wide, 5–6 mm thick, the endocarp light brown, the surface foveolate.

Distribution. Endemic to Madagascar (Fig. 27).

Habitat. *Tambourissa uapacifolia* is currently known from three collections. The type is from southeastern Madagascar at 1,000 to 1,400 m, presumably in *Tambourissa/Weinmannia* wet forest where Humbert also collected *T. capuronii* and *T. hildebrandtii.* The other two collections are from near Moromanga, probably in the same vegetation type. Additional collections and field data are obviously needed.

MADAGASCAR. TAMATAVE: S of Moromanga, 9 Feb. 1930 (fl), *Decary 7042* (P); Moromanga to Andasibe (Perinet), pk 51, 26 Oct. 1953 (fr), *Anon. in SF-7805* (P).

Tambourissa uapacifolia belongs to species Group 1A, which also includes *T. trichophylla* and *T. thouvenotii* (for which Humbert apparently mistook it). It is distinguishable from the previous two species by its larger and laxer inflorescence with longer floral pedicels, smaller bracteoles, stamens with scattered hairs on the loculi, unprolonged connectives, and by its obtuse leaves with entire margins resembling those of certain species of *Uapaca* (Euphorbiaceae).

4. Tambourissa nitida Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 34: 280. 1928; Cavaco in Humbert, Fl. Madagascar 80: 25. 1959. TYPE: Madagascar. Diego Suarez: S of Biramanja (Ambilobe), ca. 1927 (fl, fr), *Ursch 267* (holotype, P; isotype, P).

Small tree attaining 6 m tall, the new growth pilose-hirsute, the mature leafy stems 1.5–4.5 mm diam., blackish brown, hirsutulous. Leaves glabrous, opposite, petiolate; petioles 10–16 mm by 1–1.5 mm; lamina chartaceous to subcoriaceous, ovate to narrowly ovate, elliptic, rarely oblong, 60–110 mm by 26–40 mm, the apex long acuminate, ± recurved, the base acutely decurrent, the secondary veins 6–9 pairs, making a 60–70° angle with the costa, the venation prominent on both surfaces, visible to 3° adaxially and to 4° abaxially, the adaxial surface highly lustrous, the abaxial surface dull, the margin slightly revolute. Inflorescence axillary, a sexually mixed pleiochasium of 3–5 flowers, or the flowers solitary, the axes hirsute-canescent with pale, simple hairs; floral axis 5–12 mm by 1 mm, subtended by several subulate-naviculate, hirsute bracteoles 1.5–2 mm long. Androecious flower in bud globose, 6–7 mm diam., sparsely pubescent, apiculate with 3–4 narrowly deltoid, hirsute tepals, the pedicel 3–4 mm by 1–1.5 mm, subtended by a bracteole; androecious flower at anthesis unknown; stamens in bud ca. 60, ellipsoid to clavate, 1–1.5 mm long by 0.5 mm wide, the loculi separate, lateral, occupying ca. ½ total length of the stamen, connivent at the obtuse apex, the connective not prolonged, the internal receptacle surface with scattered groups of simple hairs between the stamens. Gynoecious flower at anthesis unknown, in bud turbinate or napiform, 6.5–8 mm diam. by 4–5 mm long, usually with two low, basal longitudinal ridges, externally hirsutulous-canescent, apiculate with 3–4 acute tepals; styles numerous, ca. several hundred, conical or clavate, 0.7–0.9 mm long by 0.3 mm diam., medially ventricose, the apex abruptly acuminate, the internal receptacle surface velutinous, the hairs slightly shorter than the styles. Mature fruiting receptacle unknown. Immature malformed fruit axillary on the leafy stem, ± napiform, ca. 15 mm diam., externally blackish and corky brown, pubescent, the internal surface hirsute, the scattered styles broadly conical, tapering to an acuminate apex, 0.5–0.6 mm wide by 0.8–1 mm long; pedicel and peduncle stout, obconical, 10–12 mm long by ca. 5 mm diam. medially. Carpels unknown.

Distribution. Endemic to Madagascar (Fig. 27).

Habitat. *Tambourissa nitida* is only known from two collections, both from the Sambirano region of Diego Suarez near the northern tip of Madagascar. The area where both collections originated appears to represent a transition zone between wet and deciduous forest.

MADAGASCAR. DIEGO SUAREZ: Ifazy Valley, Aug. 1909, *Perrier de la Bâthie 10126* (P).

Tambourissa nitida belongs to species Group

1B. Although the slight ridges on the female receptacles are reminiscent of *T. floricostata, T. nitida* is easily distinguishable because of its adaxially lustrous leaves with long acuminate, recurved apices. Also, its gynoecious flowers are more densely velutinous internally and its stamens lack the prolonged connectives of most allied species. Mature flowers, fruiting receptacles, as well as the habitat of this remarkable species are unknown.

5. Tambourissa hildebrandtii Perk. in Perk. & Gilg, Pflanzenr. 4, 101: 69, fig. 18:N–P. 1901; Perk., Gatt. Monim. fig. 34:N–P. 1925; Cavaco in Humbert, Fl. Madagascar 80: 29. 1959. TYPE: Madagascar. Tananarive: North Betsileo (Ant-) Sirabe, Aug. 1880 (fl), *Hildebrandt 3563* (lectotype, K, here designated; isolectotypes, BM; G, 2 sheets; P, 2 sheets).

T. baroni Drake in Grandidier, Hist. Phys. Madagascar 1(1): 24. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 41. 1911; Cavaco, Bull. Soc. Bot. France 104: 284, figs. 2, 5. 1957; Cavaco in Humbert, Fl. Madagascar 80: 26, fig. VII:5–7. 1959. TYPE: Central Madagascar. Without precise locality (ca. 1890), *Baron 2954* (lectotype, K, here designated; isolectotype, P).

T. quadrifida sensu Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902, pro parte, non Sonn.

Monoecious tree attaining 10 m tall and 30–40 cm D.B.H., the bark thin, gray, flaking, the new growth villous to velutinous with straight or matted simple hairs, the mature leafy stems 1.5–3 mm diam., dark brown, villous, glabrescent. Leaves opposite to subopposite, petiolate; petioles villous-hirsute, 4–12 mm by 1–1.2 mm; lamina chartaceous to subcoriaceous, sparsely pilose abaxially, more densely so along the costa and major veins, adaxially glabrescent, ovate, elliptic to narrowly elliptic, oblong or narrowly oblong, lorate or rarely obovate, 40–115(–135) mm by 17–44 mm, the apex shortly acuminate, shortly acute, obtuse or emarginate, the base acute to obtuse, sometimes slightly decurrent, the secondary veins 4–9 pairs, making a 55–80° angle with the costa, the venation visible to 2(–3°) adaxially, to 3(–4°) abaxially, the margin thickened, slightly revolute. Inflorescence terminal, axillary or ramiflorous, cinereous, velutinous-tomentose, a unisexual or sexually mixed pleiochasium of 3–7(–9) flowers, usually terminated by a single gynoecious flower, the floral axis 5–30 mm by 1.2–2 mm, the axis and pedicels subtended by naviculate-subulate bracteoles 1–3.5 mm long. Androecious flower in bud finely cinereous-tomentose, globose to globose-depressed, 6–7 mm diam. by 5–6 mm long, apiculate with 4 narrowly acute tepals ca. 1 mm long, the pedicel 8–10 mm by 0.6–1 mm; at anthesis deeply 4-fid, 15–18 mm diam., the lobes spreading flat; stamens ca. 75–90, deltoid to ovoid-ellipsoid, slightly recurved, 1.2–2 mm long by 0.8–1.2 mm wide, the loculi ± unilateral, introrse, separate, occupying ⅔–¾ total length of the stamen, the filament subsessile, the internal receptacle surface with scattered to dense simple hairs between the stamens. Gynoecious flower in bud subglobose-napiform, more densely tomentose than androecious flower, apiculate with 4 acutely deltoid tepals, the pedicel 10–15 mm by 1–1.2 mm; at anthesis 7–9 mm diam. by 5–6 mm long, the orifice X-shaped, 3–3.5 mm diam., splitting into 4 deltoid, suberect to outcurved lobes; styles numerous, ca. 150–200, narrowly conical, 1–1.5 mm long by 0.4–0.6 mm wide basally, the surface strongly papillose, the internal receptacle surface densely velutinous-tomentose between the styles. Fruiting receptacle usually solitary on leafless stems, ± shallowly cupuliform, 30–50 mm diam. by 20–35 mm long, the cavity shallow to almost absent, the external surface pale, mottled corky brown, the orifice comprising ⅓–½ total width of the fruit, subentire, the walls 15–25 mm thick, the internal surface with scattered, narrowly conical papillose styles 0.5–0.7 mm long by 0.5 mm wide basally, interspersed with scattered to dense hairs; pedicel and peduncle tapered, to 55 mm long by 4–5 mm diam. medially. Mature carpels 7–8 mm long, 4–5 mm wide, 3–4 mm thick, ovoid-compressed, the endocarp light brown, the surface scrobiculate.

Distribution. Endemic to Madagascar (Fig. 27).

Habitat. Tambourissa hildebrandtii displays a wide ecological amplitude comparable to that of *T. purpurea.* It ranges from the *Tambourissa/Weinmannia* montane wet forest zone above 800 m in the eastern region, to montane forests of the central plateau (ca. 1,000–1,400 m) and extends to the dry semideciduous forests of the western domain where it finally disappears.

MADAGASCAR. FIANARANTSOA: Fianarantsoa (fr), *Anon. sub SF 2145* (MAD); Inselbergs W of Ambalavao, at Pk 475, 970 m, 31 Jan. 1975 (fl, fr), *Croat 30194* (MAD, MO); National Route no. 7 at 11 km

W of Ambalavao, 950 m, 5 Nov. 1978 (fl, fr), *Lorence 2043* (MAD, MAU, MO). MAJUNGA: Natural reserve no. 8, Namoraka (Saolala), 7 Feb. 1951 (fr), *Anon. sub RN 3298* (MAD). TAMATAVE: Ambatondrazaka (near Lake Alaotra) (fl, fr), *Anon. sub. SF 1723* (MAD); Ambohijanahary, 1,000 m (by Lake Alaotra), 5 Jan. 1945 (fl), *Anon. sub SF 2188* (MAD); small forest at Marovato, East Manaka (near Lake Alaotra), 13 Nov. 1946 (fl), *Anon. sub Herb. Alaotra 3102* (MAD, 2 sheets); Didy Forest, Ambatondrazaka (near Lake Alaotra), ca. 1,200 m, 5 July 1952 (st), *Anon. sub SF 5498* (MAD); 2 June 1952 (fl), *Botoalma sub SF 4145* (MAD, 2 sheets); Andevorante, Moramanga, 5 Oct. 1912 (fl), *Afzelius s.n.* (K). TANANARIVE: Finoarive, 1,400–1,600 m, 18 Mar. 1930 (fl, fr), *Decary 7633* (K, 2 sheets); Bongolave, 800–900 m, Tsiroanandidy, July 1974 (fr), *Morat 4608* (MAD). TULEAR: upper basin of the Mandrare River (SE), pass and summit of Marosoui, 1,000–1,400 m, 14–15 Nov. 1928 (fr), *Humbert 6606* (B). PROVINCE UNCERTAIN: Arkotreano, forest N of the road to Nickelville, 29 Dec. 1944 (fl, fr), *Anon. sub Herb. Alaotra 2091* (MAD, 2 sheets); Menavavakely, Mevatanana, 16 Apr. 1951 (fl), *Anon. sub SF 3588* (MAD). WITHOUT PRECISE LOCALITY: Central Madagascar, Jan. 1882 (fr), *Baron 1144* (K, P, syntypes of *T. baroni*); (fl), *Baron 2417* (K, P); 1883 (fl), *Baron 2477* (K).

Tambourissa hildebrandtii belongs to species Group 1B and is distinguishable from other members of the group, notably its closest ally, *T. nosybensis,* by its strongly papillose styles, fruiting receptacle with a very small to almost nonexistent central cavity, and its villous stems. The type of *T. baroni* has fewer flowers and smaller, more obtuse leaves than that of *T. hildebrandtii,* but easily falls within the range of variation displayed by the species. A comparable degree of variation in leaf size and shape frequently occurs on a single individual (e.g., *Lorence 2043,* MAD, MAU, MO).

Fresh flowers of *Tambourissa hildebrandtii* are externally grayish green to peach colored. The gynoecious flowers have purple styles, whereas the androecious flowers are beefy red within and produce a sweet, fruity odor. In mixed inflorescences, anthesis occurred in gynoecious flowers before it occurred in androecious flowers (*Lorence 2043*).

Vernacular names. Ambora, Ambora saha (Madagascar).

6. **Tambourissa nosybensis** Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 302, pl. 3, figs. 12, 13. 1982. TYPE: Madagascar. Diego Suarez: Nosy Be Island (Nossi-Bé); Lokobe, Natural Reserve no. 6, 350 m, 12 Dec. 1967 (fl), *Bernardi 11847* (holotype, G; isotypes, K, P, Z).

Monoecious to subdioecious tree 6 m tall, the bark pale gray, licheniferous, longitudinally fissured, the new growth pilose with short, fulvous hairs, the mature leafy stems terete, 2–3.5 mm diam., brown, pilosulous. Leaves opposite, petiolate; petioles 6–11 mm by 1–1.2 mm, pilose-pubescent; mature lamina adaxially glabrescent, abaxially sparsely hirsutulous, especially along the costa and major veins, brown, discolorous, subcoriaceous, narrowly elliptic to narrowly oblong, occasionally ± falcate, 60–125 mm by 20–36 mm, the apex acuminate, the base acutely cuneate, the secondary veins 4–6 pairs, making a 35–45° angle with the costa, the intersecondary and tertiary branches straight with strong admedial orientation, ± perpendicular to the costa, the venation visible to 2(–3°) adaxially, and to 3(–4°) abaxially, the margin slightly revolute, thickened. Inflorescence cauliflorous, moderately to densely fulvous velutinous, a unisexual or rarely sexually mixed pleiochasium of 9–12 flowers, the floral axis 50–87 mm by 2 mm, the pedicel and peduncle 7–20 mm by 1–2 mm, the joint swollen, subtended by a caducous, subulate-naviculate bracteole 1–2 mm long. Androecious flower in bud unknown; at anthesis deeply 5-fid, 17 mm diam., the lobes thick, spreading flat, the receptacle externally hirsute; stamens ca. 70, incurved, ovoid-acuminate, subsessile, 1.5–2 mm long by 0.7–1 mm wide, the loculi lateral, separate, the connective acute, prolonged for ca. 0.5 mm, the internal receptacle surface with rare, scattered hairs among the stamens; pedicel ca. 2 mm diam. Gynoecious flower in bud discoid-patelliform, 9–10 mm diam. by 3–4 mm long, longitudinally multi-ribbed, velutinous, the apex depressed, with 4 subulate tepals ca. 1 mm long, the pedicel 9–20 mm by 1–1.2 mm; at anthesis splitting apically into 4(–6) short, straight or incurved deltoid lobes, the orifice small, X-shaped; styles numerous, ca. 400, broadly conical to columnar, apiculate, 0.4–0.6 mm long by 0.4–0.5 mm diam. basally, not papillose, the internal receptacle surface velutinous between the styles. Fruiting receptacle unknown. Figure 28.

Distribution. Known only from Nosy Be Island off the northwestern coast of Madagascar (Fig. 29).

Habitat. *Tambourissa nosybensis* was collected in depauperate lower montane wet forest (presumably of Chlaenaceae, Myristicaceae, and *Anthostema*) at 350 m.

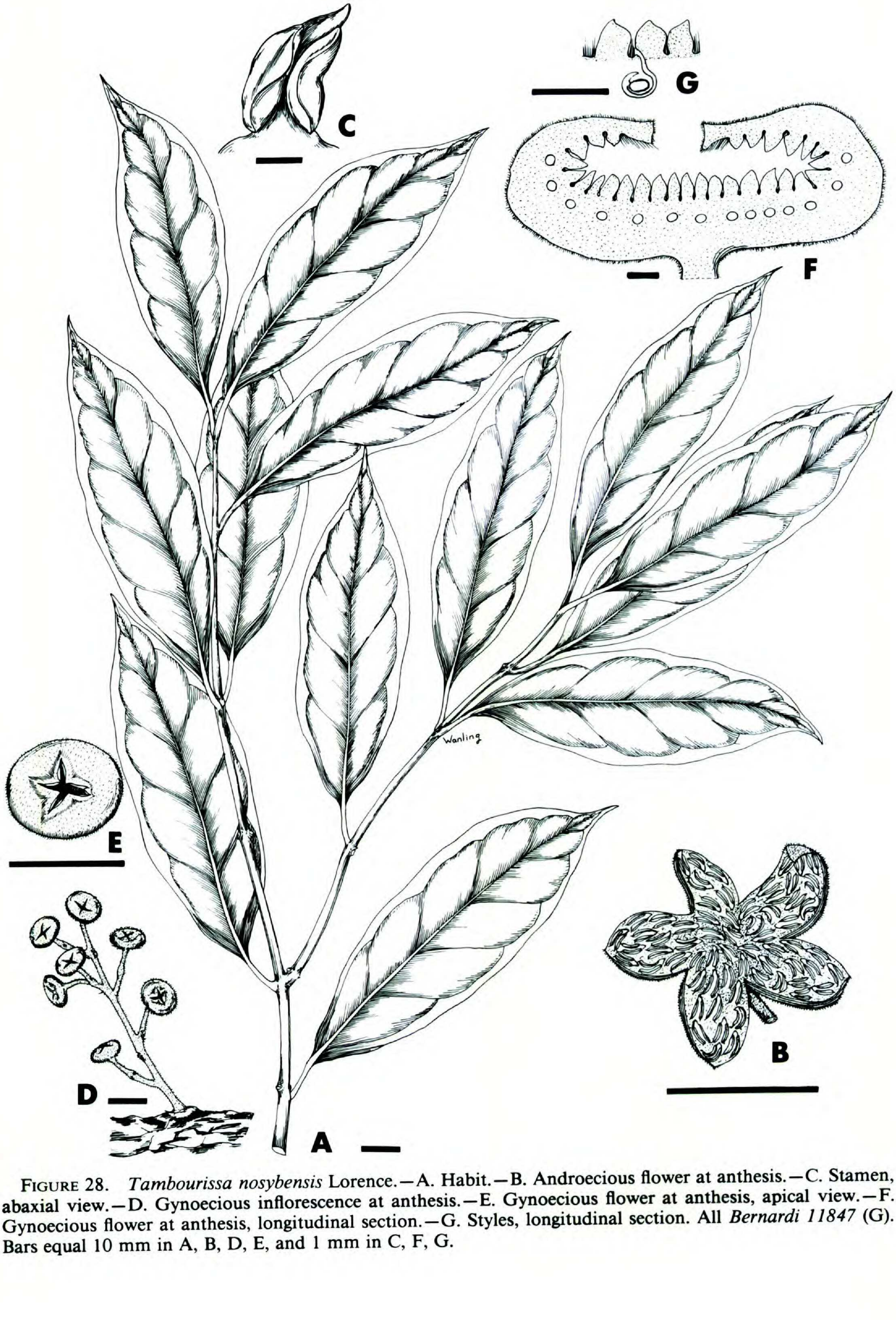

FIGURE 28. *Tambourissa nosybensis* Lorence.—A. Habit.—B. Androecious flower at anthesis.—C. Stamen, abaxial view.—D. Gynoecious inflorescence at anthesis.—E. Gynoecious flower at anthesis, apical view.—F. Gynoecious flower at anthesis, longitudinal section.—G. Styles, longitudinal section. All *Bernardi 11847* (G). Bars equal 10 mm in A, B, D, E, and 1 mm in C, F, G.

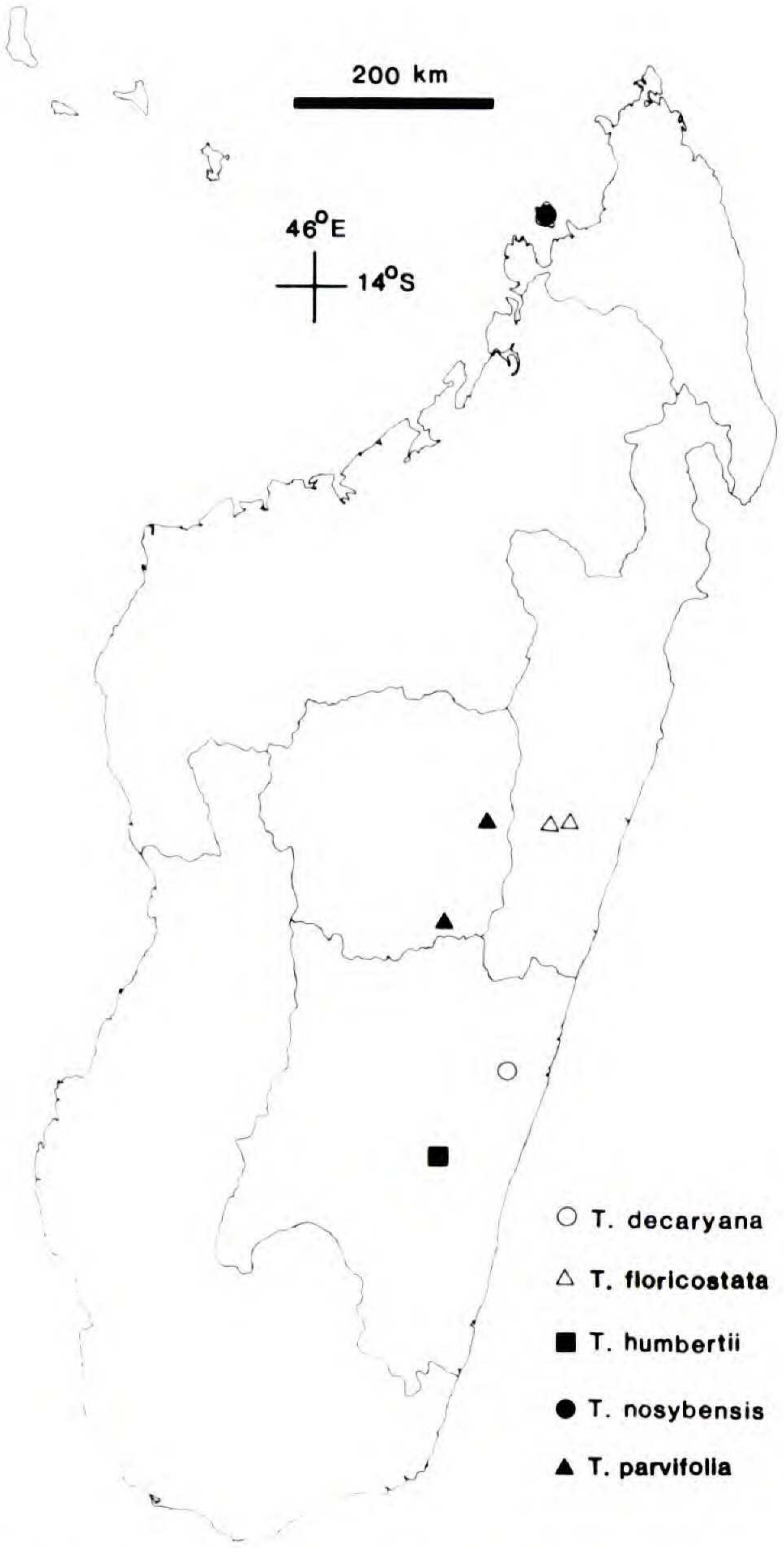

FIGURE 29. Distribution map of some *Tambourissa* species in Madagascar.

MADAGASCAR. WITHOUT PRECISE LOCALITY: ca. 1883 (fl), *Humbolt 642* (K, P).

Tambourissa nosybensis belongs to species Group 1B. Although most closely allied to *T. hildebrandtii* (for which Bernardi mistook it), *T. nosybensis* possesses sufficient distinguishing characters to merit specific status (Table 15). These include a number of specialized features, notably the production of a mucilaginous exudate in the mature gynoecious flowers (conspicuous in rehydrated flowers), and also an apparent trend towards dioecy. I first thought the species was dioecious but then found a single androecious flower among some 34 gynoecious flowers, suggesting it is monoecious. Further collections, particularly of androecious flowers and fruit, and observations on the biology of this interesting species are required.

7. **Tambourissa decaryana** Cavaco, Bull. Mus. Hist. Nat. (Paris), Ser. 2, 29: 287. 1957; Cavaco in Humbert, Fl. Madagascar 80: 22, fig. VI:1–4. 1959. TYPE: **Madagascar. Tamatave: Mt. Vatovavy (Mananjary), 22 Nov.** 1938 (fl, fr), *Decary 13697* (holotype, P).

Cauliflorous tree 10–16 m tall, possibly dioecious (?), the new growth pilose-strigillose, the adult leafy stems terete, pilose, 4–5 mm diam. Leaves opposite, petiolate; petioles 15–20 mm by 2–4 mm, pilose; lamina subcoriaceous, oblong, 150–325 mm by 85–115 mm, adaxially glabrous, abaxially strigillose with white, appressed hairs, the apex acuminate, the base obtuse to rounded, the secondary veins 6–14 pairs, making a 60–70° angle with the costa, the venation prominent, visible to 4° on both surfaces, the margin slightly revolute. Androecious flowers unknown. Gynoecious inflorescence cauliflorous, a fulvous, tomentose or velutinous pleiochasium of 6–11 flowers, the floral axis (10–)30–135 mm by 1.5–3 mm, subtended basally by several deltoid-naviculate bracteoles ca. 1 mm long, the pedicel 6–23 mm by 1–1.5 mm, subtended by a velutinous subulate bracteole (1–)4–5 mm long. Gynoecious flowers in bud napiform-depressed, 7–8 mm diam. by 4–5 mm long, externally tomentose to velutinous, the apex apiculate with 4–5 minute velutinous tepals; at anthesis 8–11 mm diam. by 7–8 mm long, the orifice shallowly 4–5-fid, comprising ½–¾ total width of the receptacle, the lobes suberect, the margins thickened; styles numerous, ca. 200–300, shortly conical, 0.4–0.5 mm long by 0.2–0.3 mm wide, basally ± ventricose, the apex acute, slightly papillose, the ovule amphitropous; receptacle lobes bearing internally several series of larger, sterile, hirsutulous conical appendages (ca. 25–40), these 1–1.5 mm long by 0.5–0.8 mm diam., the internal receptacle surface densely velutinous between the styles and on the lobes. Fruiting receptacle produced on the trunk and branches, cupuliform, 40–50 mm long by 50–70 mm diam., externally corky, the orifice comprising ⅕–⅓ total width of fruit, the styles conical, 0.5 mm long, interspersed with hairs; pedicel and peduncle 37–110 mm by 6–9 mm.

Distribution. Endemic to Madagascar (Fig. 29).

Habitat. *Tambourissa decaryana* occurs in the lower altitude Myristicaceae/*Anthostema* wet forest zone in the eastern domain, from ca. 250 to 500 m.

TABLE 15. Some distinguishing morphological features of *Tambourissa hildebrandtii* and *T. nosybensis.*

Character	*T. hildebrandtii*	*T. nosybensis*
Angle of secondary veins to costa	55–80°	35–45°
Intersecondary veins and tertiary branches	zig-zag, weak admedial orientation	straight, strong admedial orientation
Inflorescence position	ramiflorous or axillary	cauliflorous
Inflorescence pubescence	cinereous, hirsute, or tomentose	fulvous, velutinous
Stamens	outcurved	incurved
Loculi	unilateral	bilateral
Connective	short, obtuse, or absent	acute, 0.5 mm long
Gynoecious receptacle	subglobose-napiform, not longitudinally ribbed	discoid-patelliform, longitudinally ribbed
Orifice lobes	4, suberect to everted	4(–6), incurved or straight
Styles	narrowly conical, 1–1.5 mm long, strongly papillose	broadly conical to columnar, apiculate, 0.4–0.6 mm long, not papillose
Ovule	anatropous, pendulous	amphitropous, oblique
Mucilaginous exudate	absent	present, covering styles
Tanniferous cells	present	absent
Stone cells	absent	present

MADAGASCAR. TAMATAVE: Mt. Vatovavy, Mananjary Bassin, 250 m, Aug. 1911 (fr), *Perrier de la Bâthie 10091* (P); Marolambo District, Andonabe Canton, near Ambatomitsangana, 16 Sept. 1963 (fr), *Anon. in SF-21357* (P); Ambodiriana (R.N. 1), 250–500 m, 21 Aug. 1957 (fr), *Capuron 18111-SF* (P). WITHOUT PRECISE LOCALITY: Feb. 1881 (fl), *Parker s.n.* (K).

Parker s.n. differs from the type of *Tambourissa decaryana* in having a longer, less densely pubescent floral axis, and furthermore has mature gynoecious flowers (*Decary 13697* is mostly in bud). Although *Parker s.n.* lacks leaves, the presence of large sterile appendages within the flowers, an abundance of oil cells in the receptacular ground tissue, amphitropous ovules, and production of mucilage by the styles all correspond well with the type of *T. decaryana.*

The species is characterized by a moderately to densely pubescent inflorescence, long bracteoles, 4–5-fid gynoecious flowers with an X-shaped orifice and suberect lobes, and sparsely pubescent leaves, characters which place it in species Group 1B. Its huge, macrophyllous leaves (assuming they are not from a vigorous sucker shoot) and presence of several rows of large, style-like sterile appendages surrounding the styles set it apart from all other Madagascan species, although *Tambourissa parvifolia* has similar appendages. The sterile appendages in *T. decaryana* resemble the styles but are 2–4 times larger, hirsutulous, and lack an ovule at the base. Numerous oil cells occur in the receptacular ground tissue. The species also displays certain specialized features shared with *T. nosybensis,* i.e., production of a mucilaginous exudate and a tendency towards dioecy.

8. **Tambourissa humbertii** Cavaco, Bull. Soc. Bot. France 104: 283. 1957; Cavaco in Humbert, Fl. Madagascar 80: 28, fig. IX:1–4 (non fig. VIII). 1959. TYPE: Madagascar. Fianarantsoa: high valley of the Rienana River, Matitanana Basin, 18–24 Nov. 1924 (fl), *Humbert 3593* (holotype, P; isotype P).

Large tree, the new growth velutinous, the mature leafy stems flattened, stramineate, 3.5–6 mm diam., sparsely hirsutulous, glabrescent. Leaves opposite, petiolate; petioles hirsutulous, glabrescent, 10–13 mm by 1.5–2 mm; lamina glabrous, subcoriaceous, elliptic to oblong, 82–126 mm by 35–60 mm, the apex shortly acute, the base acute, slightly decurrent, the secondary veins 6–9 pairs, making a 60–70° angle with the costa, the venation visible to 3° on both surfaces, the margin revolute, the adaxial laminar surface moderately lustrous. Dioecious? Androecious flowers unknown. Gynoecious inflorescence presumably cauliflorous, a fascicle of 2–3 flowers, or a short, 5–17-flowered pleiochasium, the floral axis stout, 30–50 mm long, lenticellar, canescent, the pedicel velutinous-canescent, jointed below the middle, the pedicel and peduncle 12–20 mm by 2–3 mm, with 1 to several velutinous, deltoid-naviculate basal bracteoles 1–2 mm long. Gynoecious flower in bud canescent, broadly napiform-depressed, 13–15 mm diam. by 5 mm long, apiculate with several minute, coalescent velutinous tepals; at anthesis broadly napiform-discoid to patelliform, 18–21 mm diam. by 6–8 mm long, the orifice X-shaped, ca. 10 mm diam., splitting for ca. ½ the length of the receptacle into 4(–5) suberect, fleshy deltoid lobes, the margins thickened; styles numerous, ca. 500 or more, densely crowded, ovoid-ventricose, 1–1.2 mm long by 0.5–0.7 mm wide basally, the apex shortly acuminate or apiculate, papillose, the surface bearing scattered simple hairs ca. 1–1.5 mm long, the internal receptacle surface velutinous between the styles and on the lobes the numerous short hairs mixed with scattered long hairs. Fruit unknown.

Distribution. Endemic to Madagascar (Fig. 29).

Habitat. Tambourissa humbertii is known only from the type collection, presumably from the *Tambourissa/Weinmannia* montane wet forest zone from ca. 1,000 to 1,400 m. Further collections of this striking species, particularly androecious flowers and fruit, and observations on its life history are needed.

In contrast to Cavaco's (1957b) statement that *Tambourissa humbertii* approaches *T. ficus* from Mauritius, I find that it differs from the latter species in several important characters. Most notably it lacks the ternate-whorled to subalternate leaves and tanniferous idioblasts in the floral ground tissue characteristic of *T. ficus. Tambourissa humbertii* appears rather to belong to species Group 1B and is distinguishable from other members of the group by its much larger gynoecious flowers and presence of long hairs on the styles. Styles of *T. kirkii* (Group 2B; Comores), incidentally, bear similar but shorter scattered hairs. In addition, the internal surface of the gynoecious receptacle of *T. humbertii* bears mixed long and short hairs, a feature found in no other species.

In spite of their relatively large size, gynoecious flowers of *Tambourissa humbertii* structurally most closely resemble those of *T. decaryana.* In both species the orifice lobe margins are conspicuously thickened and numerous oil cells occur in the ground tissue. Flowers of *T. humbertii* are much larger, however, and lack the peculiar sterile appendages characteristic of the latter species.

9. Tambourissa floricostata Cavaco, Bull. Soc. Bot. France 105: 39. 1958; Cavaco in Humbert, Fl. Madagascar 80: 40, fig. IV:7–11. 1959. TYPE: Madagascar. Tamatave: Analamazaotra forest, Feb. 1919 (fl), *Ramanantoavolana sub T. Thouvenot 134* (holotype, P; isotypes, P, 2 sheets).

Schrameckia madagascariensis Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 28: 249. 1922 non *Tambourissa madagascariensis* Cavaco, 1957.

Monoecious tree 18–20 m tall, the new growth unknown, the mature growth subglabrous, the mature leafy stems terete, 1.5–2 mm diam. Leaves opposite to subopposite, petiolate; petioles 7–13 mm by 0.8–1 mm; lamina subcoriaceous to coriaceous, glabrous, elliptic to obovate, rarely oblong, occasionally slightly falcate basally, 35–85 mm by 15–36 mm, the apex obtuse to retuse, its extremity usually thickened or apiculate, the base acutely cuneate to acutely decurrent, the secondary veins 4–7 pairs, making a 55–60° angle with the costa, the venation visible to 3° adaxially and to 4° abaxially, the margin thickened, slightly revolute. Inflorescence ramiflorous, a puberulent, sexually mixed pleiochasium of (3–)5–9 flowers attaining 120–160 mm by 60–70 mm, axillary or on leafless nodes, or the flowers solitary and axillary or terminal, the floral axis (17–)23–140 mm by 1–3 mm, ± flattened, often leafy. Androecious flower in bud quadrangular-globose, 9–12 mm diam., with 2–4 prominent longitudinal ridges, apiculate with 4 deltoid-rounded hirsute tepals; pedicels 16–30 mm by 1–1.5 mm, flattened, puberulent, each subtended by a naviculate-deltoid bracteole; at anthesis 4-fid, 25 mm diam., splitting to ca. ½–⅔ total length of the receptacle, the lobes incurved, not spreading, each lobe with ca. 2 fleshy, obtuse scale-like tepals internally near the apex; stamens 16–22, large, ovoid to deltoid, acute, 3–4.5 mm long by 1.5–2.5 mm wide, the loculi lateral, free, the connective broad, ± sessile, the apex apiculate, acute, the internal receptacle surface ± glabrous. Gynoecious flowers solitary and axillary or terminal on the mixed inflorescence, the receptacle globose-depressed, 13–18 mm diam. by 5–7 mm long in bud, with 2 lateral ridges, the orifice small, 1–2 mm diam., flanked by 4 obtuse, decussate tepals; pedicels to 55 mm by 2 mm. Immature fruiting receptacle ca. 47 mm diam., broadly napiform-depressed, the orifice ca. 5 mm diam., subentire, the external surface corky brown, the internal surface with numerous scattered, shortly conical styles ca. 0.5–1 mm long by 0.5 mm wide basally, the surface between the styles hirsute. Submature fruiting receptacle solitary on leafless stems, shallowly cupuliform, 20 mm long by 45–57 mm diam., externally venose, corky, the pedicel and peduncle tapered, 120–150 mm by 4–5 mm; mature carpels unknown.

Distribution. Endemic to Madagascar (Fig. 29).

Habitat. Known only from three collections, all from the Perinet area (Analamazaotra), in the *Tambourissa/Weinmannia* wet forest zone from ca. 900 to 950 m. *Thouvenot 134* was collected in February with flowers and young fruit. As the Analamazaotra forest is included in a nature reserve, it is probable that *T. floricostata* still occurs there; much intact forest still remained in 1978. However, additional flowering and fruiting collections and data on its life history are needed.

MADAGASCAR. TAMATAVE: Analamazaotra, Feb. 1912 (seed), *Perrier de la Bâthie 10128* (P); Zedsiadra (or Djedsiatsa?) near Perinet (st), *Schedl 40* (MAD).

In spite of the large size and small number of stamens in androecious flowers of *Tambourissa floricostata,* the species possesses a number of attributes which suggest inclusion in species Group 1C, along with *T. parvifolia* (Table 5). It differs from the latter species by its larger leaves, flowers, and receptacles with two to four prominent external longitudinal ridges.

Vernacular names. Ambora, Ambora lahy, Ambora vavy (Madagascar).

10. Tambourissa parvifolia Baker, J. Bot. n.s. 11: 267. 1882; Baillon, Bull. Mens. Soc. Linn. Paris 1: 342. 1882; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911; Cavaco in Humbert, Fl. Madagascar 80: 36, fig. X:1–4. 1959. TYPE: Madagascar. Without precise locality ("Central Madagascar," probably Tananarive): 1880 (fl), *Parker s.n.* (holotype, K).

T. quadrifida sensu Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902, pro parte, non Sonn.

Monoecious treelet or tree 5–15 m tall, the new growth sparsely hirsutulous, glabrescent, the mature leafy stems 1.5–3.5 mm diam. Leaves opposite, petiolate; petioles 3–5 mm by 0.7–1 mm; lamina glabrous, coriaceous, elliptic to oblong or obovate, 15–47 mm by 9–22 mm, the apex obtuse to retuse, the base acutely cuneate to obtuse, slightly decurrent, the secondary veins 4–5 pairs, making a 55–60° angle with the costa, the venation obscure adaxially or the 2° veins scarcely visible, abaxially visible to 3°, the margin revolute. Inflorescence ramiflorous on leafless stems, an (always?) unisexual, hirtellous-puberulent pleiochasium of 2–11 flowers, the floral axis 12–70 mm by 1–2 mm, basally bracteolate. Androecious flower in bud globose, 5–6 mm diam., apiculate with several minute, coalescent tepals, the pedicel 6–10 mm by 1–2 mm, subtended by a deltoid, hirsute bracteole 2 mm long by 1 mm wide; at anthesis deeply 4-fid, 17–30 mm diam., the lobes spreading flat, the internal receptacle surface bearing several sterile, columnar appendages near the apex of the lobes; stamens ca. 50–60, ± ligulate, 1–1.5 mm long by 0.6–0.8 mm wide, the loculi lateral, free, parallel, comprising ca. ¾ total length of the stamen, the connective not or only slightly prolonged, the internal receptacle surface glabrous. Gynoecious receptacle at anthesis subglobose to napiform, ca. 9–10 mm diam., externally hirsutulous-pubescent, the orifice small, 4-lobed, X-shaped, comprising ca. ¼ total width of the receptacle, the pedicel 7–14 mm long; styles numerous, ca. 200 or more, conical, ca. 0.5 mm long by 0.5 mm wide basally. Fruiting receptacle solitary or in pleiochasia of 2 or more, the axis to 60 mm by 5 mm, hirtellous, the receptacle shallowly cupuliform to napiform-depressed, 30–95 mm wide by 25–40 mm long, the orifice comprising ca. ¼–½ total width of the receptacle, 8–12 mm wide, subentire with several thick, irregularly deltoid lobes, these bearing a number of sterile, clavate appendages 1–2 mm long on their internal surface, the external receptacle surface irregularly reddish brown with pale corky patches, glabrous or sparsely hirsutulous, the internal surface with numerous conical styles 0.3–0.5 mm long and wide basally with scattered simple hairs in between, the pedicel 10–22 mm by 3.5–6 mm. Carpels 5–13 mm long by 5–9 mm wide by 3–4 mm thick, ovoid-compressed, the endocarp tan, the surface scrobiculate.

Distribution. Endemic to Madagascar (Fig. 29).

Habitat. *Tambourissa parvifolia* is restricted to the sclerophyllous montane forest zone of the central plateau at elevations from ca. 1,400 to 2,000 m.

MADAGASCAR. ANTANANARIVO: E of Antsirabe, 2,000 m, 3–4 Nov. 1928 (fl), *Humbert 6351bis* (P); E slope of Ankaratra, 24–26 Mar. 1958 (fl), *Capuron 18507-*

SF (P). FIANARANTSOA: Andringitra, Imaisoa, 1,500–2,000 m, 28 Oct. 1960 (fl), *Leandri et al. 3393* (P). WITHOUT PRECISE LOCALITY: Central Madagascar, 1855 (fr), *Baron 3864* (BM, K, P); (st), *Baron 4204* (P); (fr), *Baron 4205* (K); (fr), *Baron 6048* (P); (fl), *Parker s.n.* (P, 5 sheets).

The sclerophyllous leaves of *Tambourissa parvifolia* are smallest of any known species of *Tambourissa* and probably represent an adaptation to the high altitude montane habitat. In fact, sclerophylly characterizes the majority of arborescent species occurring in this habitat in Madagascar, which has been termed the "forêt dense sclerophylle de montagne" (Koechlin et al., 1974).

In spite of its extremely reduced leaves, *Tambourissa parvifolia* is best placed in species Group 1C along with *T. floricostata.* It displays a number of specialized trends, including reduced leaves, a tendency towards unisexual inflorescences (and possibly dioecy) and the presence of sterile, style-like appendages on the internal surfaces of the receptacle lobes, a feature shared with *T. decaryana. Tambourissa parvifolia* is easily distinguished from *T. floricostata* by its small, obutse or emarginate leaves and slender anther filaments.

Vernacular names. Ambora, Amboravato (Madagascar).

11. Tambourissa beanjadensis Lorence, nom. nov. *Ephippiandra capuronii* Cavaco, Bull. Soc. Bot. France 104: 610. 1957; Cavaco in Humbert, Fl. Madagascar 80: 8, fig. I:10–12. 1959 non *Tambourissa capuronii* Cavaco, Bull. Mus. Hist. Nat. (Paris), Ser. 2, 29: 287. 1957. TYPE: Madagascar. Diego Suarez: Beanjada Massif (N of the Masoala Peninsula), E forest at its upper limits ("forêt des cimes"), ca. 1,100 m, 30 Dec. 1953 (fl), *Capuron 8826 bis-SF* (holotype, P).

Medium-sized monoecious tree, the new growth with rare, scattered hairs, the mature leafy stems glabrous, brown, 1.5–2 mm diam. Leaves glabrous, opposite to subopposite, petiolate; petioles 6–9 mm by 1 mm; lamina chartaceous to subcoriaceous, adaxially lustrous, minutely punctate, elliptic, (23–)34–47 mm by (12–)18–28 mm, the apex abruptly and shortly acuminate, the tip thickened, the base cuneate to broadly cuneate, rarely obtuse, the secondary veins 3–5 pairs, making a 75–85° angle with the costa, adaxially scarcely visible, abaxially prominent, the venation visible to 3° abaxially, the margin entire, slightly revolute. Inflorescence ramiflorous or cauliflorous, solitary or clustered, an apparently unisexual pleiochasium of 3–7 flowers, or the flowers rarely solitary, the floral axis 20–40 mm by 1 mm, pilose when young, glabrescent, subtended by several minute, naviculate bracteoles 1 mm long, the pedicel 3–7 mm by 1 mm, subtended by a minute, obtuse naviculate bracteole ca. 1 mm long. Androecious flower in bud globose, 4 mm diam., glabrous, the apex with 4 sparsely pilose obtuse tepals; at anthesis deeply (3–)4(–5)-fid, 8–10 mm diam., the lobes spreading flat, each bearing internally near the apex a small, scale-like tepal 1 mm wide; stamens ca. 35–36, obtuse to deltoid, 0.6–1 mm long and wide, the filament short or sessile, the loculi confluent apically into a single, crescentiform loculus occupying ⅔ or more of the total length of the stamen, the connective thick, not prolonged, the internal receptacle surface glabrous. Gynoecious flower in bud globose-napiform, ca. 6 mm diam. by 4–5 mm long, glabrous, the apex with 4 minutely puberulent obtuse tepals; at anthesis splitting into an X-shaped orifice ca. 1–2 mm wide, the 4 lobes deltoid, the internal receptacle surface with a pubescent ring near the orifice; styles numerous, ca. 200, shortly and broadly conical, 0.3–0.4 mm long and wide, papillose, producing a mucilaginous exudate, the internal receptacle surface with scattered hairs between the styles, the receptacle wall 1 mm thick. Fruiting receptacle unknown.

Distribution. Endemic to Madagascar (Fig. 30).

Habitat. The species is known only from the type collection from the upper limits of what is presumably mid altitude *Tambourissa/Weinmannia* wet forest on mountainous summits. Further collections and field observations are obviously needed.

Features which immediately place this species in the genus *Tambourissa* are the closed, globose gynoecious floral receptacle with an X-shaped orifice and the conical carpels completely immersed in and fused with the receptacle wall. The broadly deltoid, sessile stamens with a single, crescentiform loculus and presence of tepals on the inner surface of the androecious receptacle lobes occur in a number of other *Tambourissa* species, as previously noted. Pollen of the species, figured by Walker (1976) and presumably taken from the type, also conforms to that of *Tambourissa* rather than that of *Ephippiandra*.

The small leaves and ramiflorous to cauliflorous, pleiochasial inflorescence of *Tambourissa beanjadensis* resemble those of *T. parvifolia*, which differs by its more coriaceous, obtuse leaves, much larger androecious flowers, and longer stamens with distinct filaments and separate loculi. *Tambourissa beanjadensis* is probably best placed in species Group 2A, however, a diverse series of species from Madagascar, Réunion, and the Comores characterized by their deeply 4-fid androecious flowers which spread flat open and have stamens with unprolonged connectives. Its gynoecious flowers, like those of the two Réunion species in this subgroup (*T. crassa* and *T. elliptica*) are globose-depressed, open by an X-shaped orifice, are nearly glabrous within, and produce a mucilaginous exudate. Both latter species are easily distinguished by their much larger leaves, obtusely columnar styles, and stamens with separate thecae.

12. **Tambourissa madagascariensis** Cavaco, Bull. Soc. Bot. France 104: 283. 1957; Cavaco in Humbert, Fl. Madagascar 80: 30, fig. IX:5–8. 1959. TYPE: Madagascar. Majunga: Natural Reserve no. 4 (Tsaratanana, Ambanja), Mangindrano Canton, Bealanana District, 7 July 1953 (fl), *Rababoto sub R.N. 6028* (holotype, P).

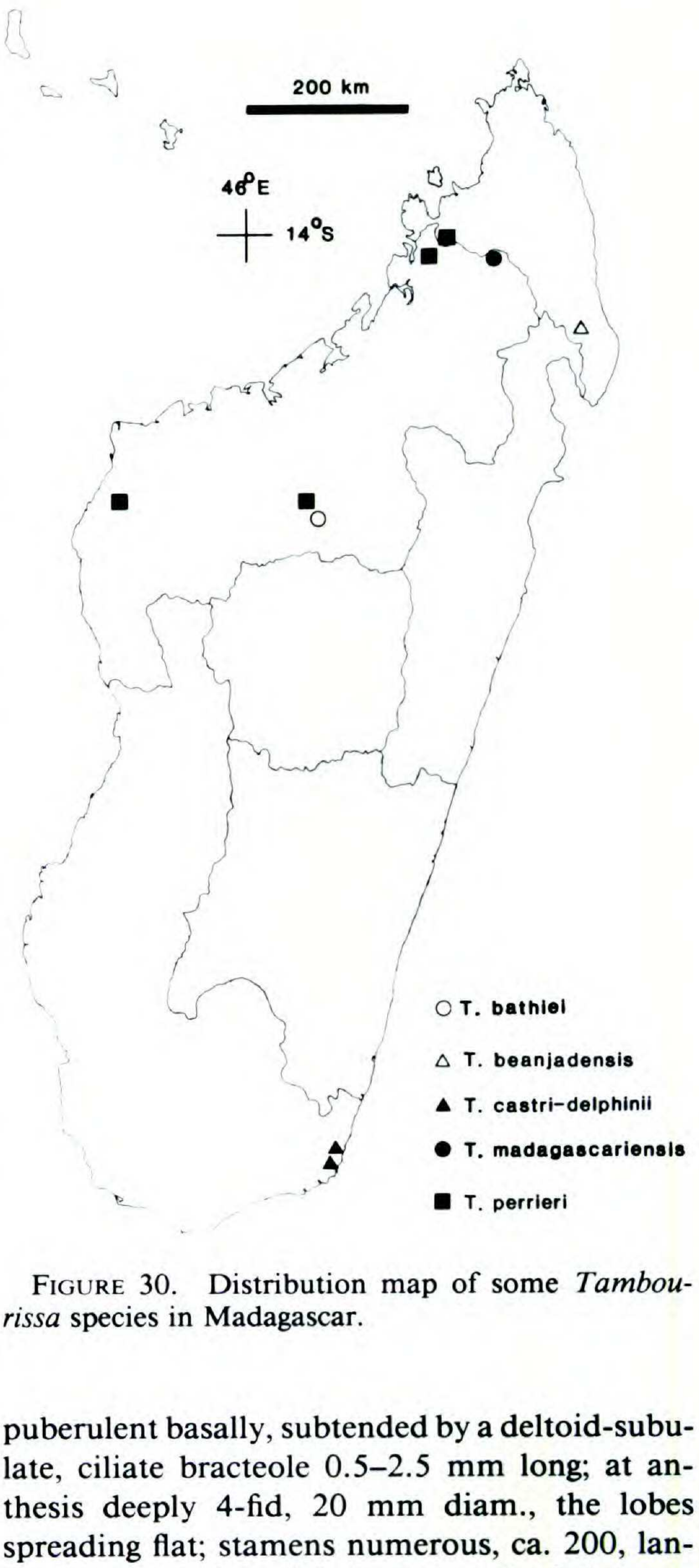

FIGURE 30. Distribution map of some *Tambourissa* species in Madagascar.

Dioecious (?) tree 5–15 m tall, or a lianescent shrub, the new growth with scattered hairs, glabrescent, the mature leafy stems glabrous, 2–3 mm diam., with longitudinal striations. Leaves glabrous, opposite to subopposite, petiolate; petioles 4–7 mm by 1–1.5 mm; lamina chartaceous, broadly elliptic, 42–80 mm by 24–34 mm, the apex acuminate, the tip ± indurated, the base acutely or rarely obtusely decurrent, the secondary veins 5–7 pairs, making a 60–70° angle with the costa, the venation obscure, visible to 2° adaxially and to 3° abaxially, the margin plane to slightly revolute. Inflorescence ramiflorous, axillary or on leafless nodes, a subglabrous unisexual pleiochasium of 3–9 flowers, sometimes leafy in the terminal portion, the floral axis 20–85 mm by 1–2 mm, longitudinally striate, sparsely puberulent around the pedicels, subtended by several broadly deltoid, ciliate bracteoles. Androecious flower in bud globose, 6–7 mm diam., ± glabrous, apiculate, the tepals fused, the pedicel 8–23 mm by 0.6–1 mm, glabrous or sparsely puberulent basally, subtended by a deltoid-subulate, ciliate bracteole 0.5–2.5 mm long; at anthesis deeply 4-fid, 20 mm diam., the lobes spreading flat; stamens numerous, ca. 200, lanceolate to subulate, 2.5–4 mm long by 0.7–1 mm wide, sessile or with a short filament, the loculi lateral, separate, occupying almost the entire length of the stamen, the connective slightly prolonged, obtusely apiculate, the internal receptacle surface glabrous. Gynoecious flower in bud subglobose, slightly depressed apically, 4–5 mm diam., externally glabrous to sparsely hirsutulous; at anthesis (?) 5–6 mm diam., the orifice circular, entire, 2–3 mm diam., comprising ca. ½ total width of the receptacle; styles numerous, several hundred, shortly columnar, 0.2–0.3 mm long, the apex rounded, the internal receptacle surface puberulent around the orifice and between the styles, the pedicel 6–8 mm long, shorter than in the androecious flower. Mature fruiting receptacle cupuliform, attaining 150 mm diam. (fide notes on *Anon. sub SF 2126*, MAD); carpels unknown.

Distribution. Endemic to Madagascar (Fig. 30).

Habitat. The type of *Tambourissa madagascariensis* was collected on the Tsaratanana massif (northern Madagascar), presumably in montane wet forest of *Tambourissa/Weinmannia* above 1,000 m. The three other known collections of this species are from montane *Tambourissa/Weinmannia* wet forest (800–1,000 m), and Myristicaceae/*Anthostema* wet forest (ca. 400–800 m) in the eastern region. This seemingly disjunct distribution pattern may be the result of undercollecting.

MADAGASCAR. TAMATAVE: Mt. Ambatosoratra, 400 m, 4 Jan. 1949 (fl), *Anon. sub Herb. Alaotra 3247* (MAD); forest N of the road to Nickelville, on the banks of the Amkotreano River, 29 Dec. 1944 (fr), *Anon. sub Herb. Alaotra 2126* (MAD); wooded area on the summit of Mt. Analavorikely, 29 Dec. 1944 (fr), *Anon. sub Herb. Alaotra 2142* (MAD).

Tambourissa madagascariensis is anomalous in a number of respects and does not readily fit into any of the more or less natural groups of Madagascan species, but is best placed in species Group 2A. Its small, thin glabrous leaves are reminiscent of *T. purpurea* and *T. gracilis*, but the flowers are borne in long, slender subglabrous and long-pedicelled pleiochasia that are more suggestive of *T. gracilis*, *T. beanjadensis*, and *T. parvifolia*. Androecious flowers of *T. madagascariensis* are relatively large, however, and split open into four lobes which spread flat and bear numerous (ca. 200) long stamens with separate, parallel loculi, thus differing strikingly from the small, globular, nearly closed androecious flowers of *T. gracilis* and *T. purpurea*, which have short, sessile stamens with apically confluent loculi.

Gynoecious flowers of *Tambourissa madagascariensis* are small and globose-depressed with an entire, circular orifice that is internally puberulent, and numerous short, columnar-rounded styles suggestive of those species which produce copious mucilage at anthesis. The orifice apparently remains open throughout much of the floral development, thus differing markedly from the gynoecious flowers of *T. beanjadensis* and *T. parvifolia* (unknown in *T. gracilis*), which open by an X-shaped orifice at anthesis and, furthermore have conical styles.

In terms of both androecious and gynoecious floral structure, *Tambourissa madagascariensis* appears to be most closely related to two of the Comorean species in Group 2A, *T. comorensis* and *T. leptophylla*, although their leaves and flowers are much larger. Presence of abundant oil cells in the gynoecious floral ground tissue of all three species and large fruits are common features. This group of Comorean species could have been derived from a common ancestor similar to *T. madagascariensis*.

Tambourissa madagascariensis also appears to share characters of androecious and gynoecious floral morphology with *T. elliptica* subsp. *micrantha* from Réunion, notably the pleiochasial inflorescence, similar androecious flowers and stamens, and gynoecious flowers with short, columnar styles and a mucilaginous exudate. Gynoecious flowers of the latter species lack the open, circular orifice, however.

Vernacular names. Ambora, Mahimasina, Valiramarnia (Madagascar).

13. **Tambourissa elliptica** (Tul.) A.DC., Prodr. 16(2): 660. 1868; Cordem., Fl. Réunion 301. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 71. 1901. *Ambora elliptica* Tul., Ann. Sci. Nat. (Paris) 4(3): 31. 1855; Tul., Monogr. Monim. 304. 1855. TYPE: Réunion. Woods of the Hauts de la Rivière des Galets, July 1851 (fr), *Boivin s.n.* (holotype, P).

Tambourissa amplifolia sensu Cordem., Fl. Réunion 301. 1895 non (Boj. ex Tul.) A.DC.

Treelet or tree of variable habit, attaining 12 m tall, the new growth glabrous or with sparse, scattered hairs, the mature leafy stems terete, 2–6(–8) mm diam. Leaves glabrous, opposite to subopposite, petiolate; petioles (8–)10–25 mm by 1.5–5 mm; lamina chartaceous to coriaceous, narrowly to broadly elliptic, oblong, obovate-elliptic, obovate, broadly obovate or orbiculate, (50–)80–180(–250) mm by (15–)25–140(–190) mm, the apex shortly acuminate, acute, obtuse or rarely rounded, the base acutely decurrent, acutely cuneate to obtuse, truncate or subcordate, the secondary veins (5–)6–12 pairs, making a 55–75° angle with the costa, the venation prominent, raised, visible to 3–4(–5°) adaxially, to 4–5(–6°) abaxially, the margin plane to slightly revolute. Leaves of seedlings and suckers heterophyllous, small and apically dentate in subsp. *elliptica,* long, narrow and entire in subsp. *micrantha.* Inflorescence subglabrous, a short ramiflorous pleiochasium (in subsp. *micrantha*), or the flowers solitary, sometimes axillary (in both subspecies), or cauliflorous and the flowers solitary or in fascicles of 2–3 (in subsp. *elliptica*). Androecious flower in bud globose, 7–15 mm diam., apiculate with 4 minute, obtuse tepals, the pedicel 10–40(–60) mm by 1–1.5 mm; at anthesis (3–)4(–5)-fid, 16–45 mm diam., the lobes spreading flat; stamens numerous, 65–300, ligulate to linear-ellipsoid, 1.5–6.5 mm long by 0.5–1 mm wide, the filament distinct, the loculi lateral, comprising ⅔–¾ total length of the stamen, separate or confluent at the obtuse apex, the connective not prolonged, the internal receptacle surface glabrous. Gynoecious flower in bud globose-depressed to napiform-depressed, apiculate with several pairs of minute tepals, the pedicel (5–)10–20(–40) mm by 0.6–2 mm; at anthesis 6–15 mm diam., the orifice X-shaped, 1–5 mm wide, splitting into 4 shallowly deltoid lobes; styles numerous, ca. 150–200 or more, bluntly columnar, polyhedral, 0. 5 mm long by 0.2–0.5 mm wide, the internal receptacle surface glabrous or with rare scattered hairs, producing a mucilaginous exudate. Fruiting receptacle solitary or in clusters of 2–3 on the trunk (subsp. *elliptica*), or on the leafless branches (subsp. *micrantha*), urceolate-globose or cupuliform, 25–90 mm diam. by 15–50 mm long, the orifice subentire, comprising ca. ⅕–½ total width of the fruit, the external surface pale corky brown or mottled with dark patches, the internal surface subglabrous with short scattered, columnar-polyhedral styles 0.5 mm wide. Mature carpels ovoid, 9–12 mm long, 5–7 mm wide, 3–4 mm thick, the endocarp whitish (subsp. *elliptica*) or pale brown (subsp. *micrantha*).

Distribution. Endemic to the wet and cloud forest zones of Réunion Island (Fig. 31).

E. J. de Cordemoy recognized four species of *Tambourissa* in his "Flore de l'Ile de la Réunion" (1895), but used names of a Madagascan (*T. religiosa*) and a Mauritian (*T. quadrifida*) species for two endemic Réunion taxa that I have named *T. crassa* and *T. elliptica* subsp. *micrantha* respectively (Lorence, 1982).

Tambourissa elliptica, the only previously described species from Réunion, is quite polymorphic, but two modally distinct subspecies are distinguishable both by morphology, and, to a lesser degree, altitudinal distribution. Both subspecies are monoecious with pink or pale yellowish white flower color morphs (never dark purple as is *T. crassa*), caulinary flowers, conspicuous higher order venation, contain stone cells in the floral ground tissue, and have a less well-developed hypodermis than in *T. crassa,* the second Réunion species.

Subspecies *elliptica* consists of a series of mostly mid to upper elevation forms which Cordemoy considered to represent two distinct species (*T. elliptica* and *T. amplifolia,* respectively), based on leaf characters which prove to be variable. Subspecies *micrantha* usually occurs at lower elevations, particularly in the southeastern part of the island where the most lowland wet forest still remains.

Each subspecies tends to occupy its own altitudinal zone throughout much of Réunion (Fig. 31), at least in higher altitude wet and cloud forest, significant portions of which are still preserved due to the island's accentuated relief and steep, inaccessible slopes largely unsuitable for cultivation. A thorough distributional analysis is not possible for the lowlands, however, because little natural wet forest habitat remains there.

KEY TO THE SUBSPECIES OF *TAMBOURISSA ELLIPTICA*

1a. Flowers large, usually solitary or fasciculate, cauliflorous or ramiflorous; androecious buds 13–14 mm diam.; expanded androecious flowers 30–45 mm diam., the stamens ca. (100–)200–300 in number, (3–)4–6.5 mm long; gynoecious flowers 10–12 mm diam.; fruiting receptacle 45–90 mm diam.; sparse treelets or small, slender trees; medium to high elevations (1,000–2,000 m, rarely lower) .... 13a. subsp. *elliptica*

1b. Flowers smaller, usually in pleiochasia, sometimes solitary, always ramiflorous or axillary; androecious buds 8–10 mm diam.; expanded androecious flowers 20–25(–27) mm diam.; large trees with dense crowns; lower elevations, (200–600 m, rarely higher) .... 13b. subsp. *micrantha*

13a. Tambourissa elliptica subsp. elliptica.

Monoecious or subdioecious treelet or small tree attaining 6 m tall and 25 cm D.B.H., the bark soft, corky, pale brown, the new growth glabrous, rarely with a few scattered hairs, the mature leafy stems terete, 3–6(–8) mm diam. Leaves glabrous, opposite to subopposite, petiolate; petioles 10–25 mm by 2–5 mm; lamina subcoriaceous to coriaceous, elliptic to broadly

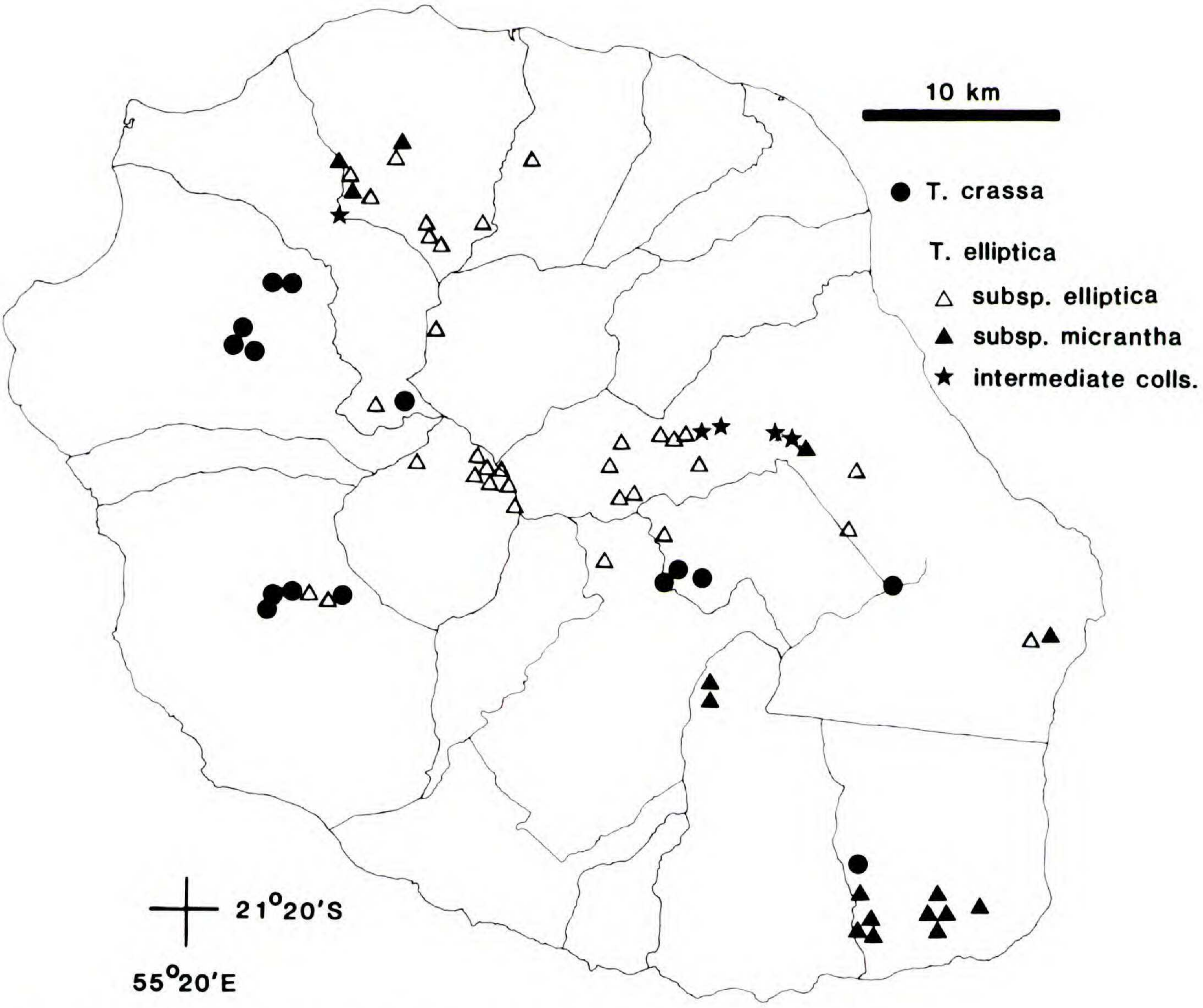

FIGURE 31. Distribution map of *Tambourissa* in Réunion.

elliptic, obovate to broadly obovate or orbiculate, 100–180(–250) mm by 60–140(–190) mm, the apex acute, rarely acuminate, obtuse or retuse, the base acute to obtuse, cuneate to decurrent, truncate or subcordate, the secondary veins 6–8 pairs, making a 55–75° angle with the costa, the venation prominent, visible to 3(–4°) adaxially and to 4(–5°) abaxially, the margin slightly revolute; juvenile and sucker leaves heterophyllous, with 1–2 pairs of glandular teeth in the apical portion of the lamina, the petiole red when living. Inflorescence glabrous or rarely with scattered hairs, the flowers solitary or in fascicles of 2–3 on meristematic swellings along the trunk, or the flowers ramiflorous and usually solitary, either axillary or on leafless nodes. Androecious flower in bud globose, (8–)12–15 mm diam., apiculate with several ± coalescent pairs of minute, glabrous tepals, the pedicel 20–40(–60) mm by 1–1.5 mm, jointed near the base with the short peduncle, subtended by several pairs of small, deltoid, decussate ciliate bracteoles; at anthesis 4(–5)-fid, 30–45 mm diam., the lobes spreading flat; stamens numerous, (100–)200–300, ellipsoid to linear, 3–5 mm long by 0.6–1 mm wide, the filament broad, distinct, comprising ca. 1/4–1/3 total length of the stamen, the loculi subparallel, lateral, connivent or confluent at the obtuse apex, comprising 2/3–3/4 total length of the stamen, the connective not prolonged, the internal receptacle surface glabrous, glaucous. Gynoecious flower in bud globose-depressed to napiform-depressed, apiculate with several pairs of minute, ± coalescent tepals, the pedicel 5–10(–40) mm by 1.2–2 mm, jointed near the base with the short peduncle, subtended by several pairs of decussate bracteoles; at anthesis 8–15 mm diam. by 5–10 mm long, the orifice 4-fid, 2–5 mm diam., X-shaped with 4 short, straight to incurved deltoid lobes; styles numerous, ca. 200 or more, bluntly columnar, ca. 0.5 mm long by 0.2–0.5 mm wide, ± polyhedral, the internal receptacle surface glabrous or with rare, scattered hairs. Fruiting receptacle solitary on the trunk or major branches, urceolate-globose, 45–90 mm diam. by 30–50 mm long, the orifice 10–30 mm diam., comprising ⅕–⅓ total width of the receptacle, subentire with remnants of the lobes, the external surface light corky brown, the internal surface glabrous, corky, with numerous short, ± polyhedral styles ca. 0.5–1 mm wide by 0.2–0.5 mm long, the apex flat or depressed, the pedicel and peduncle 10–60 mm long by 8–10 mm diam. Mature carpels ovoid-compressed, 10–12 mm long, 5–6 mm wide, 3–4 mm thick, the endocarp whitish, the surface smooth, unsculptured. Gametic chromosome number $n = 19$.

Distribution. Endemic to Réunion (Fig. 31).

Habitat. It ranges from lower montane wet forest at altitudes from ca. 200 to 1,100 m, to cloud forest at altitudes from ca. 1,100 to 2,000 m.

RÉUNION. BÉBOUR: from Bébour to Casse de Tacamaca, 1,350–1,220 m, 18 Jan. 1975 (fl), *Bernardi 15151* (G, 2 sheets; P); Bébour Plateau, 8 Nov. 1972 (fr), *Bosser 21498* (P); on Piton Rond, ca. 1,800 m (fl), *Coode et al. 4223* (K, REU); Piton Rond, 1,300–1,600 m, 23 Feb. 1979 (fl), *Lorence 2431* (MAU, MO); (fl), *Lorence 2432* (MO); (fl, fr), *Lorence 2433* (MAU, MO). BOIS BLANC: Hauts de Bois Blanc, 600 m, July 1972 (fr), *Friedmann 1891* (P). BRAS JEANNE: Oct. 1944 (st), *Rivals s.n.* (TL-R); along canal of Bras Jeanne, Oct. 1944 (st), *Rivals s.n.* (TL-R). BRÛLÉ DE ST. DENIS: Hauts du Brûlé de St. Denis, Mar. 1943 (st), *Rivals s.n.* (TL-R); Ilet à Quinquina, near St. Denis, July 1945 (st), *Rivals s.n.* (TL-R). CIRQUE DE CILAOS: Mare à Joseph forest, 1,400 m, 25 Mar. 1967 (st), *Cadet 664 bis* (REU); 19 July 1975 (fl), *Cadet 4946* (REU); 22 Feb. 1975 (fl), *Cadet 5062* (REU); Petit Matarum, 1,700 m, 22 Feb. 1975 (fl), *Cadet 5055* (REU); R bank of Bras de Benjoin, road to Cilaos, 950 m, 3 Feb. 1968 (fl), *Capuron 28002-SF* (P, 2 sheets); Mare à Joseph above Cilaos, 1,400 m, 23 Feb. 1975 (fr), *Coode 4928* (K); (fl), *Coode 4929* (K); Coteau Kerveguen cloud forest, 1,500–1,700 m, 24 Feb. 1979 (st), *Lorence & Rolland 2437* (MAU, MO); (fl), *Lorence & Rolland 2438* (MO); (fl, fr), *Lorence & Rolland 2439* (MAU, MO); (fl), *Lorence & Rolland 2440* (MAU, MO); (fl), *Lorence & Rolland 2441* (MAU, MO); (fl, fr), *Lorence & Rolland 2442* (MAU, MO); Grand Matarum and Mare à Joseph, Aug. 1943 (st), *Rivals s.n.* (TL-R); Ilet des Salazes, Cilaos, 1,300 m, 21 Feb. 1944 (fl), *Rivals s.n.* (TL-R); slopes of the Piton des Neiges, 1,900–2,000 m (fr), *Rivals s.n.* (TL-R); Mare à Joseph, 1,200 m (fr), *Rivals s.n.* (TL-R). CIRQUE DE MAFATE: Mafate, Aug. 1883 (st), *Cordemoy s.n.* (TL-R); Sentier des Scouts, from Le Belier to top of Galets Gorge, ca. 1,800 m (fl), *Richardson 4136* (K). MOKA: Moka (st), *Rivals s.n.* (TL-R); 20 Feb. 1945 (fl), *Rivals s.n.* (TL-R); Hauts de Moka at the Chabries, 600 m, Apr. 1946 (fr), *Rivals s.n.* (TL-R). LA MONTAGNE: Grande Montagne, 1,200 m, 22 Mar. 1968 (fr), *Cadet 1291* (REU). NOUVELLE: La Nouvelle, near forestry station, May 1949 (fl), *Rivals s.n.* (TL-R). PITON RAVINE À MALHEUR: heights of Piton de la Ravine à Malheur, 900 m, May 1943 (st), *Rivals s.n.* (TL-R). PLAINE D'AFFOUCHES: forest along path to Plaine d'Affouches, 900 m, May 1943 (st), *Rivals s.n.* (TL-R). ROCHE ECRITE: path to Roche Ecrite, 28 Feb. 1975 (fl), *Coode 5000* (K, 2 sheets; REU); 5 Oct. 1938 (st), *Rivals s.n.* (TL-R). PLAINE DES CAFRES: Plaine des Cafres (st), *Cordemoy s.n.* (TL-R); Piton Bleu, 26 Sept. 1882 (st), *Cordemoy s.n.* (TL-R). PLAINE DES CHICOTS: near Mamode Camp, 1,200 m, 27 Dec. 1966 (st), *Cadet 595* (REU). PLAINE DES MAKES: Domainial line above Tévelave, along edge of Plaine des Makes, Oct. 1943 (st), *Rivals s.n.* (TL-R); ravine of the Col à Maison Rouge, 28 June 1967 (st), *Cadet 1039* (REU). PLAINE DES MERLES: Salazie, 1,200 m, 19 Feb. 1944 (fl), *Rivals s.n.* (TL-R). PLAINE DES PALMISTES: Petite Plaine above Plaine des Palmistes, cloud forest, 1,200 m, 25 Feb. 1979 (fl), *Lorence & Rolland 2454* (MO); 13 Jan. 1973 (fl, fr), *Cadet 4021* (REU). SAINTE ANNE: above Sainte Anne, 1,200 m, 30 May 1974 (fr), *Cadet 4714* (REU); near Sainte Anne bridge (st), *Cordemoy s.n.* (TL-R). TAKAMAKA: Takamaka forest, Ilet à Bananes, 600–1,000 m, 10 Mar. 1979 (fl), *Lorence & Rolland 2525* (MAU, MO); (fl), *Lorence & Rolland 2526* (MO); (fl), *Lorence & Rolland 2527* (MAU, MO); (fl, fr), *Lorence & Rolland 2528* (MAU, MO); (fl), *Lorence & Rolland 2529* (MO); (fl, fr), *Lorence & Rolland 2530* (MAU, MO); path to Bras Cabot, slopes of the Ilet de Patience, 1,200–1,500 m, Feb. 1971 (fl), *Bosser 20578* (P); Grand Fond forest, Takamaka, 900 m, 23 July 1943 (st), *Rivals s.n.* (TL-R). WITHOUT PRECISE LOCALITY: 1836–1837 (fl), *Gaudichaud s.n.* (P); (st), *Rivals s.n.* (TL-R).

Both the upland and lowland forms of *Tambourissa elliptica* subsp. *elliptica* include individuals with either pink or pale greenish to yellowish white floral color morphs (as does subsp. *micrantha*), but never dark purple as in *T. crassa*. Floral odors of both *T. elliptica* subsp. *elliptica* and *T. crassa* are strong and rancid-fruity with overtones of butyric acid, never pleasantly sweet-fruity as in subsp. *micrantha*. In addition, gynoecious flowers of both subspecies of *T. elliptica* and also of *T. crassa* are morphologically similar and produce a mucilaginous exudate that partly fills the floral cup. Strong similarities in the floral construction of all three Réunion taxa suggest a fairly recent derivation from a single, common ancestor. Both species belong to Group 2A.

Although upland and lowland forms of *Tambourissa elliptica* subsp. *elliptica* are quite distinct in their extremes, they intergrade gradually and clinally. For example, collections from Takamaka (eastern Réunion) form a continuous series ranging from lowland wet forest at 600–700 m elevation, to the lower limits of cloud forest at 900–1,000 m (*Lorence & Rolland 2525–2530*, all MO). Both forms are diploids with $n = 19$. Because they are not separable by any single constant character, nor even by any constant constellation of characters, it is not possible to recognize them formally as taxa. The type of subsp. *elliptica* from the Hauts de la Rivière des Galets (*Boivin s.n.*, P) represents an intermediate form, although most closely approaches the upland type.

Vernacular names. Bois de bombarde, Bois de bombarde à grandes feuilles (Réunion).

13b. Tambourissa elliptica subsp. **micrantha** Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 298, pl. 2, fig. 8. 1982. TYPE: Réunion. Brûlé de Baril: lower montane wet forest, ca. 300 m, 2 Mar. 1979 (fl), *Lorence, Lorence & Cadet 2489* (holotype, MO; isotypes, K, MAU, P, REU, Z).

T. quadrifida sensu Cordem., Fl. Réunion 301. 1895 non Sonn.

Monoecious canopy tree 10–12 m tall and 30 cm D.B.H., the bark soft, pale yellow-brown, corky and peeling, the new growth with sparse, short simple hairs, soon glabrous, the mature leafy stems 2–5 mm diam. (to 8 mm diam. on suckers), longitudinally striate. Leaves glabrous, opposite to subopposite, petiolate; petioles (8–) 10–20 mm by 1.5–2 mm; lamina chartaceous to subcoriaceous, elliptic, narrowly elliptic, oblong or obovate-elliptic, (50–)80–180(–220) mm by (15–)25–50(–65) mm, the apex shortly acuminate, shortly acute, obtuse or rarely rounded, the base acutely cuneate to acutely decurrent, the secondary veins (5–)7–12 pairs, making a 55–65° angle with the costa, the venation prominent, finely reticulate, visible to 4(–5°) adaxially and to 5(–6°) abaxially, the margin plane to slightly revolute; juvenile and sucker leaves heterophyllous, long and narrowly elliptic, the lamina attaining 180 mm by 40 mm, the apex acute to acuminate, the secondary veins 10–14 pairs, the petiole and costa bright red when living. Inflorescence ramiflorous on old or new stems, or axillary, a unisexual or sexually mixed pleiochasium of 3–7 flowers, with sparse scattered hairs, the floral axis 8–20 mm by 1–1.5 mm, subtended by several minute, ciliate naviculate bracteoles 0.6–0.8 mm long, or the flowers rarely solitary. Androecious flower in bud globose to globose-depressed, 7–9 mm diam., the apex with 4 minute, obtuse tepals, the pedicel 10–28 mm by 1 mm, subtended by a minute bracteole; at anthesis (3–)4-fid, 16–26 mm diam., the lobes spreading flat; stamens 65–95, ligulate, 1.5–2.5 mm long, 0.5–0.8 mm wide, the filament short, the loculi lateral, comprising ca. ⅔–¾ total length of the stamen, apically connivent or confluent, the connective not prolonged. Gynoecious flower in bud napiform-depressed, apiculate with 4 minute tepals, the pedicel (5–)10–20 mm by 0.6–0.8 mm, subtended by a single bracteole; at anthesis 6–7 mm diam. by 4–6 mm long, the orifice X-shaped, 1–2 mm diam., splitting into 4 suberect deltoid lobes; styles numerous, ca. 150–160, short, bluntly columnar, 0.5 mm long by 0.3–0.4 mm wide, interspersed with rare, scattered hairs. Fruiting receptacle solitary or in clusters of 2–3 on leafless branches, cupuliform-urceolate, 25–45 mm diam. by 15–30 mm long, the orifice 6–14 mm diam., comprising ca. ⅓–½ total width of the fruit, subentire, the walls 10–15 mm thick, the external surface dark reddish brown mottled with pale corky patches, the internal surface with scattered, short, bluntly columnar-polyhedral styles ca. 0.3–0.5 mm long by 0.5 mm wide, interspersed with rare, scattered hairs, the pedicel and peduncle 12–16 mm by 3–6 mm. Mature carpels 9–11 mm long, 5–7 mm wide, 3–4 mm thick, the endocarp pale brown, the surface with rugose striations. Gametic chromosome number: $n = 19$. Figure 32.

Distribution. Endemic to Réunion (Fig. 31).

Habitat. *Tambourissa elliptica* subsp. *micrantha* is occasional to locally common from ca. 300 to 700 m in the southern sector of Réunion on the lower slopes of the active volcano, the Piton de la Fournaise (le Volcan) massif (at Basse Vallée, Brûlé de Baril, Forêt de la Mare Longue, Mare d'Arzul, and Bois Blanc). Collections are also known from l'Echo below Plaine des Palmistes (ca. 700 m), and the subspecies reaches ca. 1,000 m at Brûlé de St. Denis and Plaine d'Affouches.

RÉUNION. BOIS BLANC: 300 m, Apr. 1949 (fl), *Rivals s.n.* (TL-R). BRÛLÉ DE ST. DENIS: rainy season (Dec.–Feb.) 1945 (fr), *Rivals s.n.* (TL-R). BASSE VALLÉE: Béloni, 21 Oct. 1971 (fr), *Friedmann 3265* (P). BRÛLÉ DE BARIL: 26 Feb. 1975 (fl), *Coode et al. 4963* (K, 2 sheets; REU); 300 m, 2 Mar. 1979 (st), *Lorence, Lorence & Cadet 2487* (MAU, MO); (fl), *Lorence, Lorence & Cadet 2488* (B, K, MAU, MO, P, REU, Z); 13 July 1979 (fr), *Lorence & Cadet 2741* (MO); (fr), *Lorence & Cadet 2742* (MAU, MO); (fr), *Lorence & Cadet 2743* (B, K, MAU, MO, P, REU, Z). DOS D'ANE: 1,200 m, Mar. 1974 (fl), *Friedmann 2299* (P, intermediate form). GRAND ÉTANG: (E Réunion) ca. 500 m, 15 July 1979 (fl), *Lorence & Rolland 2758* (MO, intermediate form). L'ECHO: St. Benôit to Plaine des Palmistes route, 700 m, 4 July 1967 (st), *Cadet 1038 bis* (REU); (st), *Cadet*

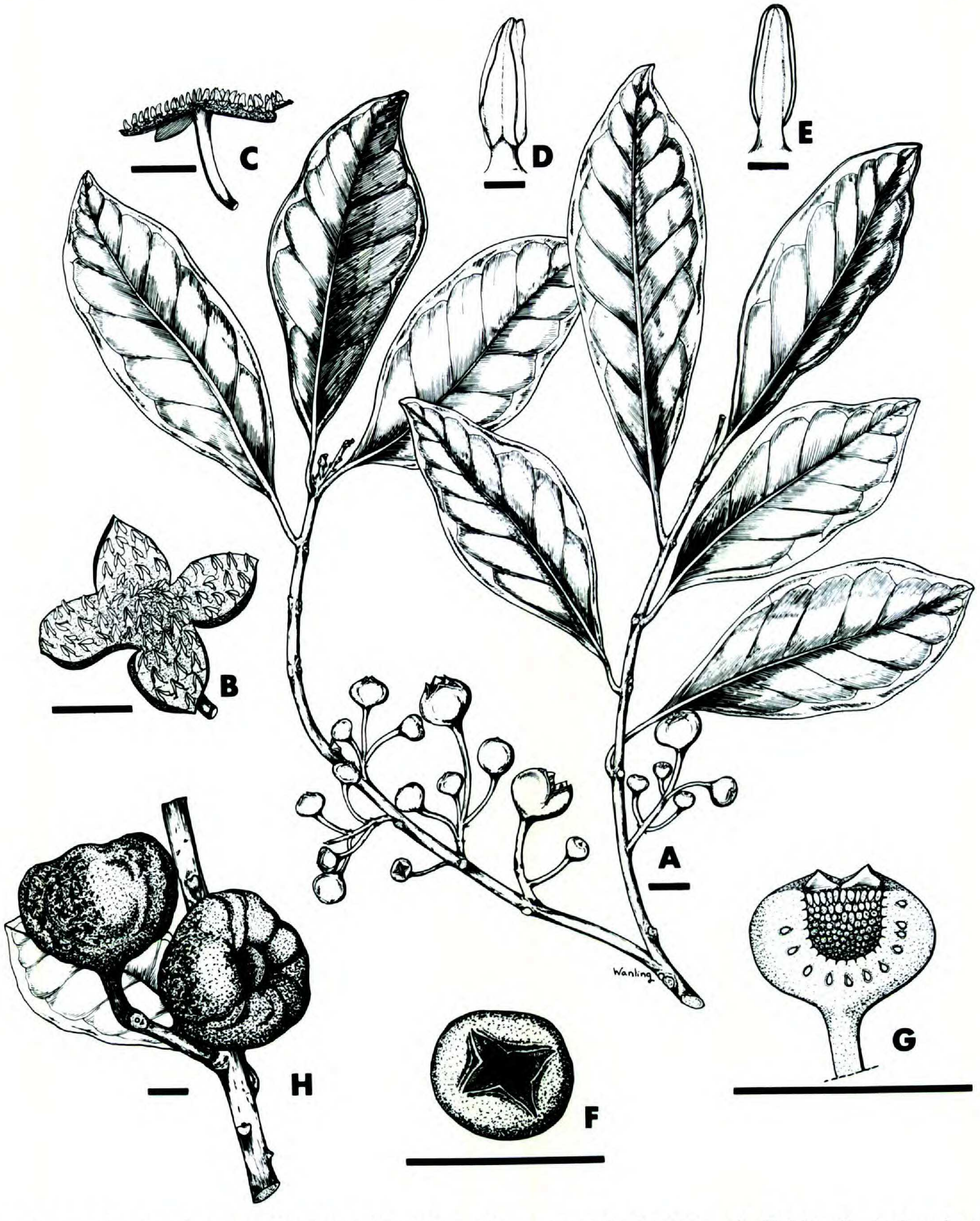

FIGURE 32. *Tambourissa elliptica* (Tul.) A.DC. subsp. *micrantha* Lorence.—A. Habit.—B. Androecious flower at anthesis, apical view.—C. Androecious flower at anthesis, lateral view.—D. Stamen, abaxial view.—E. Stamen, adaxial view.—F. Gynoecious flower at anthesis, apical view.—G. Gynoecious flower at anthesis, longitudinal section.—H. Submature fruiting receptacles. A–G. *Lorence 2489* (MO). H. *Lorence 2741* (MO). Bars equal 10 mm in A–C, F–H, and 1 mm in D, E.

1039 bis (REU, intermediate form); 27 Feb. 1979 (st), *Lorence 2462* (MO, intermediate form). PLAINE D'AFFOUCHES: La Montagne, road to Plaine d'Affouches, 1,000 m, pk 4.5, 27 Dec. 1966 (st), *Cadet 612* (REU); (fr), *Rivals s.n.* (TL-R). RIVIÈRE DES REMPARTS: high valley of the Rivière des Remparts, 1,000 m, 7 Mar. 1975 (fl), *Cadet 5123* (REU, intermediate form); 1,100 m, (fl), *Cadet 5124* (REU, intermediate form). ST. PHIL-

IPPE: Mare d'Arzul forest, 9 Dec. 1943 (st), *Rivals s.n.* (TL-R); St. Philippe (st), *Rivals s.n.* (TL-R); Mare Longue forest, 400–780 m, 14–15 Jan. 1975 (fr), *Bernardi 15044* (G, 3 sheets; P, REU); ca. 500 m, 25 Feb. 1975 (fl), *Coode et al. 4956* (K, 2 sheets; REU); 250–500 m, 2 Mar. 1979 (fl), *Lorence, Lorence & Cadet 2483* (MAU, MO); Jan. 1949 (st), *Rivals s.n.* (TL-R); May 1943 (st), *Rivals s.n.* (TL-R). TAKAMAKA: Takamaka forest, Ilet à Bananes, ca. 800–900 m, 10 Mar. 1979 (fl), *Lorence & Rolland 2524* (MO, intermediate form). WITHOUT PRECISE LOCALITY: 1853–1863 (fl, fr), *Frappier 4* (P, 5 sheets).

At Brûlé de Baril, *Tambourissa elliptica* subsp. *micrantha* becomes a subcanopy or canopy tree attaining 10–12 m with a straight trunk attaining 25–30 cm D.B.H. and a narrow, compact crown with numerous, erect branches. It differs most conspicuously from subsp. *elliptica* in having elliptic to narrowly elliptic leaves with a laminar length to width ratio exceeding 2:1 and often approaching 3:1. Juvenile and sucker leaves of subsp. *micrantha* are longer and narrower than its adult leaves, have more numerous secondary veins, bright red petioles and midribs when living, but lack dentate margins. Subspecies *elliptica* has instead apically dentate-serrate juvenile leaves, as do most other congeners for which data is available.

Flowers of both sexes are conspicuously smaller than in subsp. *elliptica,* hence the epithet *micrantha.* Large individuals of subsp. *micrantha* are monoecious, often with sexually mixed pleiochasia, whereas sex expression appears to be size and/or age related in subsp. *elliptica.* Flowers of subsp. *micrantha* are generally pleiochasial and ramiflorous or axillary, whereas those of subsp. *elliptica* tend to be cauliflorous, sometimes axillary. Fruits of subsp. *micrantha* are generally smaller, often produced in clusters of two or three on the branches, and are more conspicuously mottled in contrast to the larger, solitary and often caulinary fruits of subsp. *elliptica* which are more uniformly pale brown.

Although the two subspecies of *Tambourissa elliptica* occur together in certain areas of wet forest at low to medium altitudes (e.g., Hauts du Bois Blanc; Hauts du Brûlé de St. Denis) and remain distinct there, they intergrade in other localities, e.g., Takamaka (*Lorence & Rolland 2524,* MO), Dos d'Ane (*Friedmann 2299,* P), Rivière des Remparts (*Cadet 5123, 5124,* REU), and Grand Etang (*Lorence & Rolland 2758,* MO). Both subspecies have $n = 19$. Despite occasional intermediate collections, the two taxa are separable by relatively constant, modally distinct characters of floral size and odor, staminal length and number, ratio of laminar length to width, and fruit size. I have therefore chosen to recognize them as subspecies.

Tambourissa elliptica subsp. *micrantha* belongs to species Group 2A. In view of its monoecy, less reduced pleiochasial inflorescences, and flowers intermediate in size and number of parts, it seems to be the least specialized of the Réunion taxa and therefore probably most like the ancestral species from which the others were derived.

Vernacular names. Bois de bombarde, Bois de bombarde à petites feuilles (Réunion).

14. Tambourissa crassa Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 298, pl. 2, fig. 7. 1982. TYPE: Réunion. Road to Maïdo above Petite France, on forestry road C.F. 81; low cloud forest, ca. 1,200–1,400 m, 19 July 1979 (fl), *Lorence 2780* (holotype, MO; isotypes, K, MAU, P, REU, Z).

T. religiosa sensu Cordem., Fl. Réunion 301. 1895 non (Tul.) A.DC.

Dioecious tree, rarely shrubby, 7–8 m tall, the trunk stout, to 30 cm D.B.H., the bark pale grayish brown, smooth to irregularly fissured-flaking, the crown compact, the new growth glabrous, rarely with a few scattered hairs, the mature leafy stems 4–9 mm diam., terete, glabrous, longitudinally wrinkled. Leaves glabrous, opposite to subopposite, petiolate to subsessile; petiole stout, 4–15(–20) mm by (2–)3–6 mm; lamina coriaceous, obovate, broadly obovate, broadly elliptic or suborbiculate, (40–)60–175 mm by (20–)40–140 mm, the apex obtuse, rounded, or retuse-emarginate, the base acutely cuneate to acutely decurrent, the secondary veins 5–6 pairs, making a 45–55° angle with the costa, the venation obscure, visible to 2(–3°) adaxially and to 3(–4°) abaxially, the margin moderately revolute, the color pale brown to bright yellow-green when dry. Inflorescence a solitary monochasium terminal on the leafy stems (the subtending leaves ± caducous), or rarely cauliflorous or ramiflorous and terminal on short, leafy or leafless bracteate shoots. Androecious flower in bud globose, 13–14 mm diam., glabrous, apiculate with 4 small, obtuse-deltoid, ± glabrous tepals, the pedicel and peduncle stout, erect or recurved, 15–32 mm by 4–5 mm, bearing several caducous, ciliate deltoid bracteoles basally; at anthesis 4–5-fid, 32–45(–50) mm diam., the lobes thick, spreading almost flat or somewhat incurved, the internal receptacle surface glabrous; stamens numerous, ca. 125–250, ligulate-ellipsoid, 4–5 mm long by 1–1.5 mm wide, the filament short and thickened basally, the loculi lateral, comprising ca. ⅔–¾ total length of the stamen, usually confluent apically, occasionally free, the connective not prolonged. Gynoecious flower in bud napiform to globose-depressed, the apex with 4 small, obtuse or deltoid, glabrous or sparsely ciliate tepals, the pedicel and peduncle suberect, 8–25 mm by 2–4 mm, bearing several small, ± ciliate bracteoles basally; at anthesis urceolate-globose to urceolate-napiform, 12–14 mm diam. by 8–10 mm long, the walls thick, the apex splitting into 4(–8) thick, subequal, shallowly deltoid lobes, the orifice 5–6 mm diam., comprising ca. ¼–⅓ total width of the receptacle; styles numerous, ca. 200 or more, crowded, bluntly columnar, ca. 0.5 mm long by 0.3–0.5 mm wide, the internal receptacle surface glabrous, producing a mucilaginous exudate. Submature fruiting receptacle globose-urceolate, ca. 60 mm diam. by 40 mm long, corky brown externally, internally glabrous with numerous scattered, bluntly columnar polyhedral styles ca. 0.3 mm long by 0.5–0.8 mm wide, the pedicel and peduncle stout, ca. 50 mm by 10 mm. Mature carpels unknown. Figure 33.

Distribution. Endemic to Réunion (Fig. 31).

Habitat. *Tambourissa crassa* is local and occasional in cloud forest formations from ca. 1,200 to 2,000 m, rarely extending as low as 700 m (e.g., at Basse Vallée, *Bosser 21313*).

RÉUNION. BASSE VALLÉE: humid forest, 600–700 m, 20 Oct. 1972 (fr), *Bosser 21313* (P). BOIS DE NÈFLES: Hauts du Bois de Nèfles, St. Paul, 1,400 m, 17 Sept. 1979 (fl, fr), *Cadet 4790* (REU); (fl), *Cadet 4791* (REU). LES MARES: Les Mares, 1,500 m (fl), *Friedmann 3001* (P). MAÏDO: road to Maïdo above Petite France, 1,350 m, 22 Feb. 1979 (st), *Lorence & Cadet 2412* (MAU, MO); ca. 1,200 m, 22 Feb. 1979 (st), *Lorence & Cadet 2414* (MAU, MO). PLAINE DES CAFRES: (st), *Cordemoy s.n.* (TL-R); Col de Bellevue at Grande Montée de la Plaine des Cafres, low cloud forest, 1,600 m, 27 Feb. 1979 (fl), *Lorence 2468* (MAU, MO); (fl), *Lorence 2469* (MAU, MO); (fl), *Lorence 2470* (MO); 17 July 1979 (fl), *Lorence 2767* (K, MAU, MO, P, Z); summit of the slopes of the Grande Montée, 15 Mar. 1943 (st), *Rivals s.n.* (TL-R). PLAINE DES MAKES: 16 Mar. 1971 (st), *Friedmann 1031* (P). PLAINE DES PALMISTES: banks of the Ravine Petite à Bras des Calumets, 1,300 m, 17 Jan. 1972 (fl), *Cadet 3477* (REU). PLAINE DES SALAZES: 2,000 m, 19 Feb. 1944 (st), *Rivals s.n.* (TL-R). PLAINE DES TAMARINS: 1,800 m, below the Col de Fourche, Mafate, 28 Nov. 1974 (fl), *Cadet 4604* (REU). RIVIÈRE DE L'EST: low thicket along the Rivière de l'Est, 1,550 m, Nov. 1967 (fl), *Cadet 5717* (REU). TÉVELAVE: forestry road above Tévelave, cloud forest, 1,300–1,400 m, 28 Feb. 1979 (fl), *Lorence 2478* (MO); along the domainial line, 1,700 m, cloud forest transitional to heath formation, 6 Mar. 1979 (fl), *Lorence 2500* (MAU, MO); Hauts du Tévelave, 1,500–1,900 m (st), *Rivals s.n.* (TL-R). WITHOUT PRECISE LOCALITY: (st), *Rivals s.n.* (TL-R).

Tambourissa crassa belongs to species Group 2A and is most closely allied to *T. elliptica* subsp. *elliptica,* also from Réunion, from which it can be distinguished by its truly dioecious habit, thicker leaves, and solitary, terminal flowers and fruits borne at the ends of the top branches (rarely caulinary on short, leafy or leafless bracteate shoots, but even then solitary and terminal). The succulent, strongly discolorous leaves of *T. crassa* have a well-developed hypodermis 4–6 cell layers thick, which is only 2–3 cells thick in both subspecies of *T. elliptica.* Other distinguishing features are its somewhat pachycaulous habit, sparse and compact crown, the almost camphor-like fragrance of the dried specimens, and absence of stone cells and tanniferous idioblasts from the floral ground tissue.

Unlike the more variable *Tambourissa elliptica* subsp. *elliptica, T. crassa* is quite stable morphologically. As in most species, a certain amount of intraspecific variation occurs in leaf size and shape, flower color, and number of stamens, but both species are quite distinct morphologically. Both *T. crassa* and *T. elliptica* subsp. *elliptica* frequently occur sympatrically in the cloud forest zone (1,200–2,000 m), e.g., at Hauts du Tévelave, and along the road to Maïdo, where neither intermediates nor putative hybrids were found. For these reasons I regard *T. crassa* as a discrete species rather than a subspecies of *T. elliptica* in spite of certain morphological similarities.

Both *Tambourissa crassa* and *T. elliptica* subsp. *elliptica* have large, structurally similar leaves and large flowers with numerous stamens and styles, which are presumably adaptations to a shared habitat and similar pollinators. Apparently both taxa have evolved from a common ancestor with less specialized features, which *T. elliptica* subsp. *micrantha* appears to approach most closely. *Tambourissa crassa* has attained the highest degree of specialization of the three Réunion taxa, however, in being dioecious and having inflorescences reduced to a single, terminal flower.

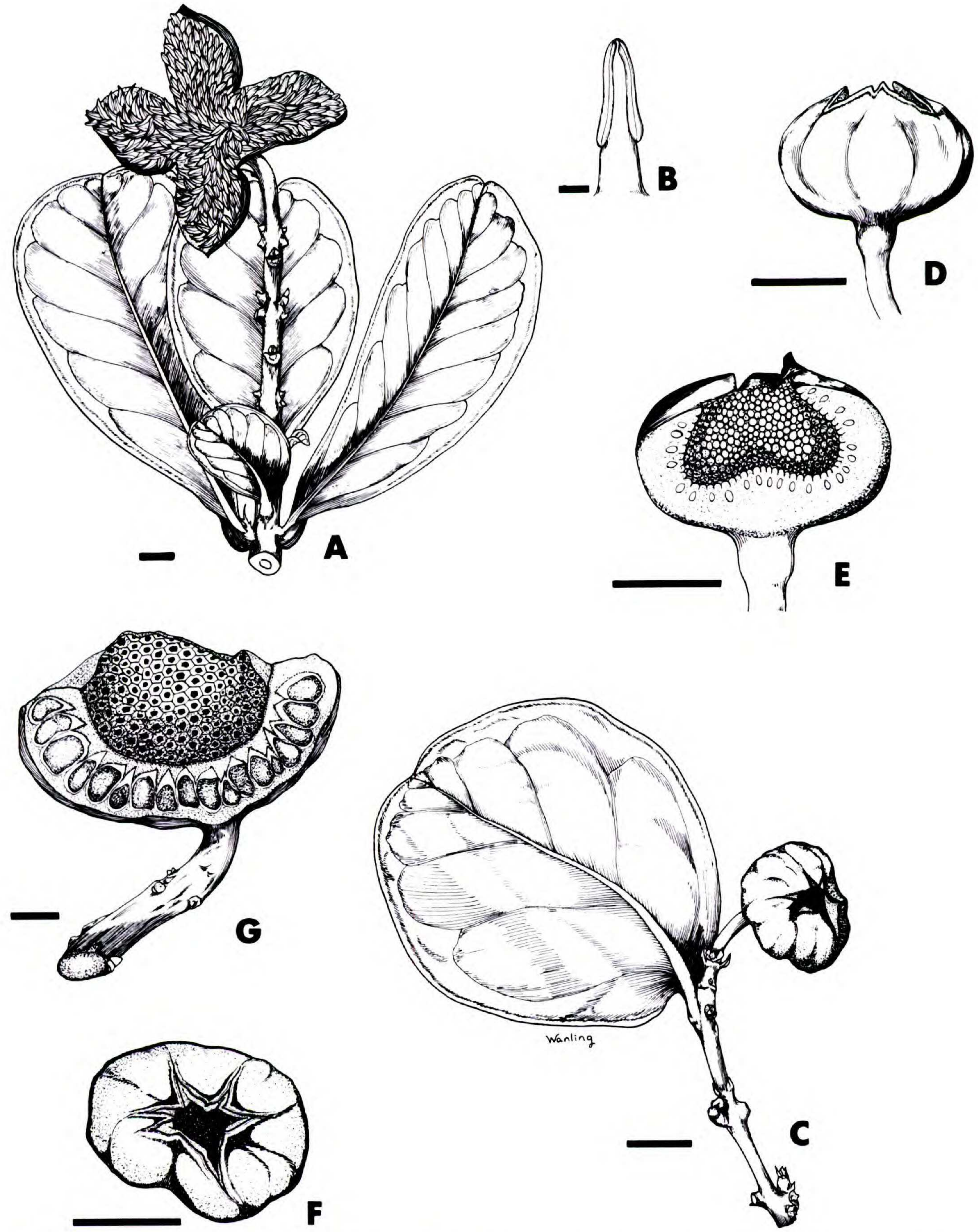

FIGURE 33. *Tambourissa crassa* Lorence.—A. Habit, with androecious flower at anthesis.—B. Stamen, adaxial view.—C. Habit, with gynoecious flower at anthesis.—D. Gynoecious flower at anthesis, lateral view.—E. Gynoecious flower at anthesis, longitudinal section.—F. Gynoecious flower at anthesis, apical view.—G. Fruiting receptacle, longitudinal section. A, B. *Lorence 2767* (MO). C–F. *Lorence 2780* (MO). G. *Cadet 4790* (REU). Bars equal 10 mm in A, C–G, and 1 mm in B.

Flowers of both sexes produce strong, rancid-fruity floral odors of butyric acid, as do those of *Tambourissa elliptica* subsp. *elliptica*. Both pale yellow-green and dark purple floral color morphs occur, although flower color appears to be constant within a given population (e.g., yellow at Col de Bellevue, purple at Hauts du Tévelave).

Vernacular names. Bois de bombarde, Bois de bombarde à grandes feuilles (Réunion).

15. Tambourissa comorensis Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 295, pl. 1, figs. 3, 4. 1982. TYPE: Comore Archipelago. Grande Comore: La Grille forest above Maoueni, ca. 800 m, 29 July 1979 (fl, fr), *Lorence & Banfi 2878* (holotype, MO; isotypes, B, G, K, MAU, P, REU, Z).

Large monoecious canopy tree 15–20 m tall and 50 cm D.B.H., the bark pale brown, smooth, flaking, the new growth glabrous or with rare, scattered hairs, the mature leafy stems pale greenish, terete, glabrous, 3–4 mm diam. Leaves opposite to subopposite, glabrous, petiolate; petiole 10–28 mm by 1–1.5 mm; lamina chartaceous, elliptic, narrowly elliptic, ovate, oblong or lanceolate, (60–)80–140 mm by (20–)30–75 mm, the apex shortly acuminate, rarely acute or obtuse, the tip rounded, the base acutely cuneate to obtuse, generally slightly decurrent, the secondary veins 4–7 pairs, making a 50–60° angle with the costa, the venation prominent, visible to 4(–5°) on both surfaces, the margin plane to slightly revolute; juvenile leaves heterophyllous, the apical ½–⅔ of the lamina serrate-dentate with 1–5 pairs of large teeth, the petiole red when living. Inflorescence cauliflorous or ramiflorous, on meristematic swellings on the trunk or on leafless nodes of the branches, a short, unisexual or sexually mixed pleiochasium of 4–9 flowers, the floral axis 5–20(–60) mm by 2–3 mm, when young finely velutinous-pubescent with short, simple or fasciculate hairs, each pedicel subtended by a minute naviculate bracteole. Androecious flower in bud globose, 9–14 mm diam., externally puberulent to glabrous, ± pustular, apiculate with a small pore flanked by 2–4 pairs of dark, hirsutulous, broadly deltoid tepals, the pedicel 8–30 mm by 1–1.5 mm; at anthesis deeply 4(–6)-fid, 23–35 mm diam., the lobes spreading flat and reflexing slightly, the apex of each lobe with several fleshy tepals internally, the internal receptacle surface glabrous; stamens numerous, ca. 125–150, linear-ligulate, 2.5–4 mm long by 0.7–1 mm wide, the loculi separate, parallel, lateral or slightly abaxial, occupying almost the entire length of the stamen, the filament short, thick, the connective not prolonged. Gynoecious flowers 1–6 per inflorescence, terminal or lateral, the pedicel 12–20 mm by 2 mm; at anthesis broadly patelliform-urceolate, 12–15 mm diam. by 5–7 mm long, the orifice circular, entire, 7–10 mm diam., comprising ⅔ total width of the receptacle, the rim velutinous, open even in bud, the external surface puberulent, ± pustular; styles numerous, several hundred, coalescent, short, bluntly columnar-polyhedral, 0.3–0.5 mm long and wide, the apex papillose, the internal receptacle surface with scattered hairs. Fruiting receptacle solitary or in clusters of 2–3 on the trunk and major branches, irregularly cupuliform, often ± distorted, 90–175 mm diam. by 50–75 mm long, the orifice comprising ca. ⅓–½ total width of the receptacle, entire, subcircular, 45–90 mm diam., the walls 16–25 mm thick, externally smooth, mottled reddish brown, internally glabrous with numerous scattered columnar-polyhedral styles 0.3–0.4 mm long by 0.5–0.8 mm wide. Mature carpels ovoid to ellipsoid, compressed, 11–13 mm long, 5–8 mm wide, 4–6 mm thick, the endocarp dark brown to black, the surface scrobiculate. Gametic chromosome number, $n = 19$. Figure 34.

Distribution. Endemic to Grande Comore (Fig. 35).

Habitat. *Tambourissa comorensis* occurs in lower montane wet forest formations. All known collections are from La Grille forest above Maoueni (northern part of the central ridge, 800–900 m), and from forest above Ntsorale Dimane along the eastern part of the same massif (250–900 m, fide Bernardi). At La Grille, I found it to be locally abundant and codominant as a subcanopy or canopy tree, striking when in fruit with numerous, large brown receptacles hanging from the trunk and branches, some split open to reveal an array of red-orange carpels set against a pale orange background. One of the largest known members of the genus, both in habit and in fruit, it flowers from August to December concurrently with the ripening of the previous year's fruit crop.

GRANDE COMORE. NTSORALE DIMANE: 250–900 m, *Nuxia* and *Weinmannia* formation, 9 Dec. 1967 (fl), *Bernardi 11803* (G, 2 sheets; K, P, Z). LA GRILLE: 850–900 m, *Tambourissa, Ocotea, Anthocleista,* and *Polyscias* formation, 1–3 Dec. 1967 (fl, fr), *Bernardi 11645* (G, 2 sheets; K, P, Z); May 1963 (fl), *Bosser 18096*

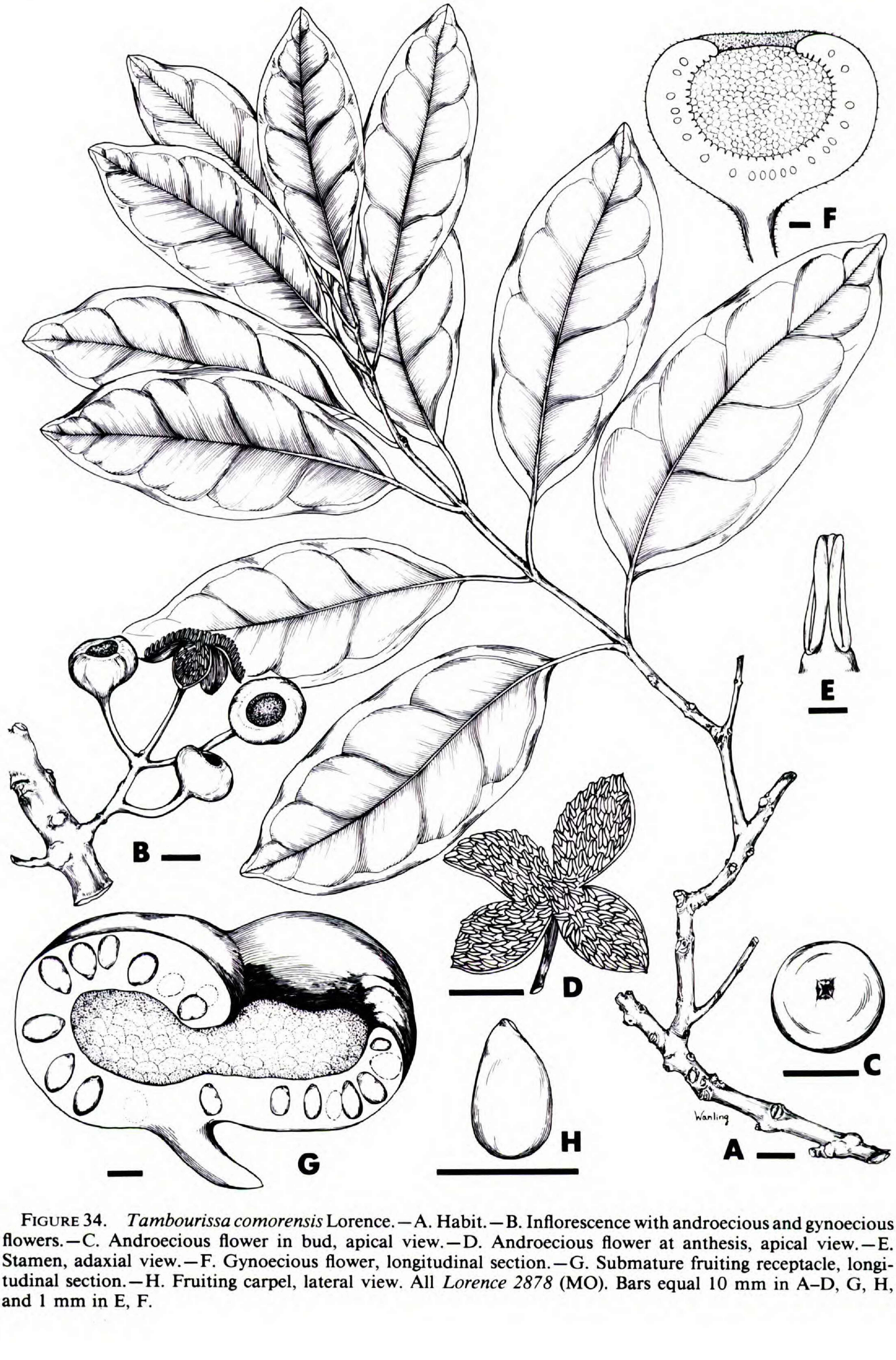

FIGURE 34. *Tambourissa comorensis* Lorence.—A. Habit.—B. Inflorescence with androecious and gynoecious flowers.—C. Androecious flower in bud, apical view.—D. Androecious flower at anthesis, apical view.—E. Stamen, adaxial view.—F. Gynoecious flower, longitudinal section.—G. Submature fruiting receptacle, longitudinal section.—H. Fruiting carpel, lateral view. All *Lorence 2878* (MO). Bars equal 10 mm in A–D, G, H, and 1 mm in E, F.

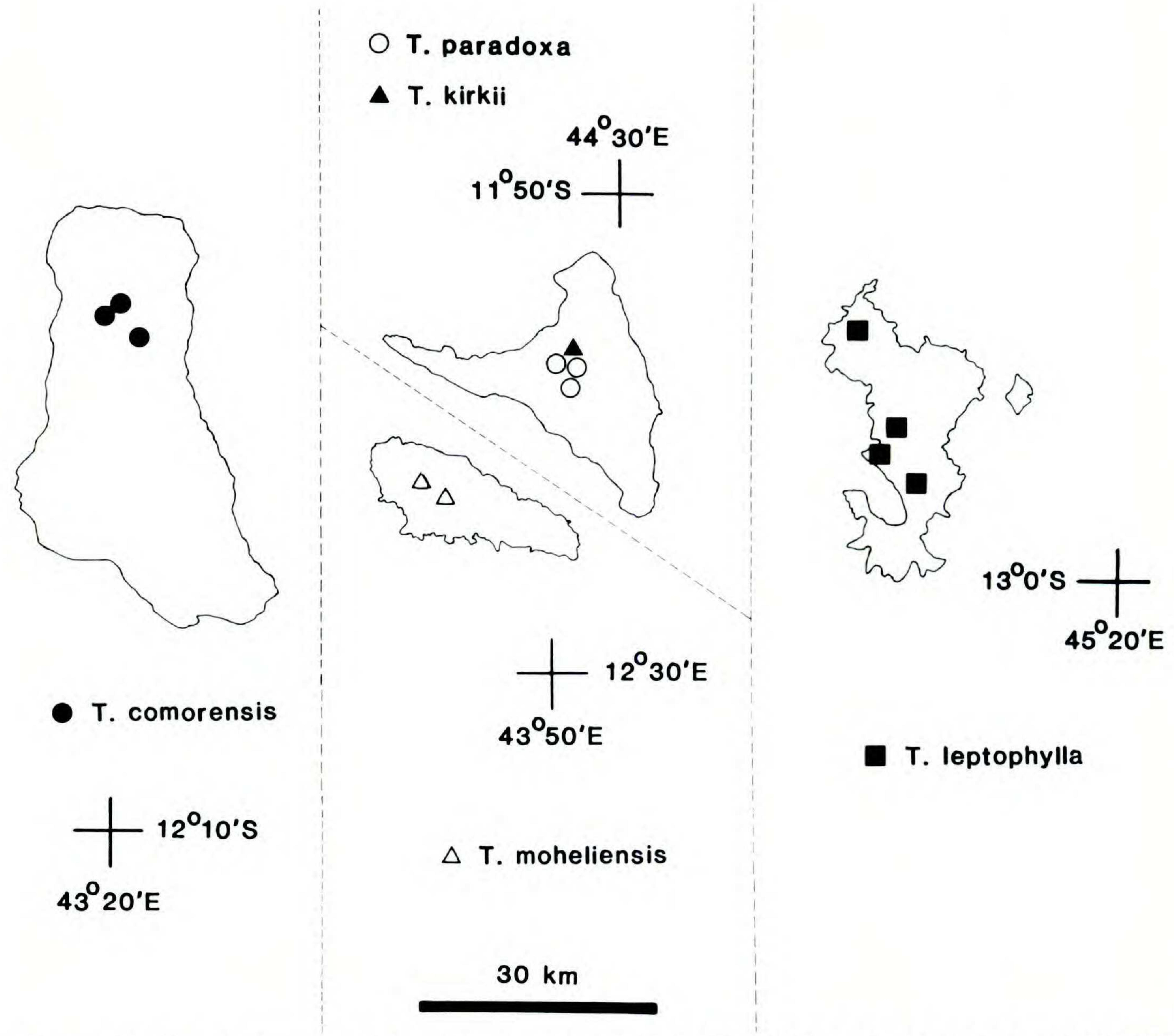

FIGURE 35. Distribution maps of *Tambourissa* in the Comore Islands (left to right): Grande Comore, Mohéli, Anjouan, Mayotte.

(MAD, P); ca. 800 m, 29 July 1979 (fr), *Lorence & Banfi 2877* (MO, K, P); 9 Feb. 1957 (fl), *Anon. in SF-16529* (P).

Tambourissa comorensis belongs to species Group 2A, also including *T. leptophylla* which differs by its smaller androecious buds, fewer stamens, and by its gynoecious receptacle with a much smaller orifice and acute, conical styles. Also, fruits of the latter are uniformly dull, corky brown externally with a smaller orifice. Dried fruits of *T. comorensis* are strongly fragrant in the herbarium, like those of *T. moheliensis* (Group 3). *Tambourissa kirkii* (Group 2B) differs by its small, globular androecious flowers, which open only partially and contain fewer stamens with acute, prolonged connectives. In living material, androecious flowers of *T. comorensis* are white and produce a pleasant, sweet odor of fermenting fruit. Buds and gynoecious flowers are pale green externally. At anthesis, gynoecious flowers have glistening, pale green styles, although massive mucilage production was not apparent. In mixed inflorescences of *Lorence & Banfi 2788,* the gynoecious flowers matured before the androecious flowers.

Vernacular name and uses. M'Bweza (Grande Comore), meaning "to calm the pain" or "to heal." Natives of Grande Comore infuse the leaves to make a medicinal tea.

16. **Tambourissa leptophylla** (Tul.) A.DC., Prodr. 16(2): 658. 1868; Baill., Hist. Pl. ed. 2, 1: 310, 344, 345. 1871; Cavaco in Humbert, Fl. Madagascar 80: 34, fig. VIII:1–4. 1959. *Ambora leptophylla* Tul., Ann. Sci.

Nat. (Paris) 4(3):29. 1855; Tul., Monogr. Monim. 298, tab. 25, fig. 1. 1855. TYPE: Comore Archipelago. Mayotte: Zuaby (ca. 1851) (fl), *Boivin 3133* (lectotype, P, here designated; isolectotypes, P, 4 sheets).

Monoecious or subdioecious tree attaining 10 m tall and 40 cm D.B.H., the bark pale brown, flaking, the new growth finely pubescent, the mature leafy stems glabrescent, terete, 3–5 mm diam. Leaves opposite to subopposite, glabrous, petiolate; petiole 15–20 mm by 1.5–2.5 mm; lamina membranaceous to chartaceous, ovate to elliptic or oblong, 120–250 mm by 60–110 mm, the apex shortly acuminate to acute, the base acute to obtuse, often slightly decurrent, the secondary veins 5–8 pairs, making a 50–65° angle with the costa, the venation visible to 4° adaxially and to 4(–5°) abaxially, the margin plane to slightly revolute; juvenile and sucker leaves heterophyllous, the margin serrate with 2–5 pairs of teeth in the apical half, the petioles red when living. Inflorescence a pleiochasium or thyrse of 7–25 flowers, sometimes leafy, cauliflorous from meristematic swellings on the trunk, or a ramiflorous pleiochasium of 5–11 flowers on the leafless nodes, or the flowers solitary and axillary, when young finely velutinous, later puberulent, the floral axis 20–150 mm by 1–3 mm, subtended by several minute, caducous bracteoles. Androecious flower in bud globose-depressed, 6–8 mm diam., smooth, the apex with 4 minute puberulent tepals, the pedicel 10–40 mm by 1–1.5 mm, subtended by a small, velutinous deltoid bracteole; at anthesis deeply 4-fid, 20–25 mm diam., the lobes spreading flat, the internal receptacle surface glabrous; stamens 80–90, linear-ligulate, recurved, 2–3 mm long by 0.8–1 mm wide, the loculi separate, parallel, occupying almost the entire length of the stamen, apically connivent or the connective slightly prolonged and apiculate. Gynoecious floral receptacle globose-patelliform, apically depressed; at anthesis 10–15 mm diam. by 5–7 mm long, the orifice entire, circular, comprising ca. ¼–⅓ total width of the receptacle, open even in bud, the rim hirsute; styles very numerous, ca. 300–600, broadly conical, 0.6–0.8 mm long by 0.3–0.5 mm wide basally, the internal receptacle surface hirsute between the styles. Fruiting receptacle solitary or in clusters of 2–4 on the trunk and major branches, globose-patelliform, apically depressed, 90–130 mm diam. by 75–90 mm long, the orifice circular, entire, 15–40 mm diam., comprising ca. ⅙–¼ total width of the receptacle, the walls 16–25 mm thick, the external surface uniformly dull, corky grayish brown, the internal surface with scattered, sharply conical styles 0.7–1 mm long by 0.5–0.8 mm wide basally, interspersed with abundant simple hairs, the pedicel and peduncle tapered, 70–80 mm long by 9–10 mm diam. medially. Mature carpels ovoid-compressed, 13–17 mm long, 8–10 mm wide, 3–6 mm thick, the endocarp light to dark brown, the surface shallowly foveolate-reticulate.

Distribution. Endemic to Mayotte, Comore Archipelago (Fig. 35).

Habitat. It is local and occasional in lower montaine evergreen wet forest formations often dominated by *Aphloia* and *Nuxia*. Recent collections are from the Benara massif (400–653 m) and also the Hachiroungou massif (400–600 m), in remnants of indigenous forest. The species also occurs in secondary forest with native remnants, the recent collections being from Barakani and Sada, both at ca. 100 m. Flowering occurs from August to September concurrently with the ripening of last year's fruits.

MAYOTTE. BARAKANI: secondary forest and along roadside, ca. 100 m, 24 July 1979 (fr), *Lorence & Saida 2824* (MO); near Barakani, Aug. 1977 (fl, fr), *Tattersall s.n.* (MO). BENARA MASSIF: E peak, wet forest on summit, ca. 600–653 m, 24 July 1979 (st), *Lorence & Saida 2828* (K, MO); (fl), *Lorence & Saida 2829* (MAU, MO, P). DZOMNOGNE: (fl), *Pobeguin 86* (P). HACHIROUNGOU MASSIF: (NW Mayotte) wet forest with *Nuxia* and *Aphloia*, ca. 400–500 m, 26 July 1979 (fr), *Lorence & Saida 2854* (K, MAU, MO, P, REU, Z). SADA: ca. 100 m, Aug. 1977 (fl), *Tattersall s.n.* (MO).

Tambourissa leptophylla belongs to species Group 2A. Its androecious flowers most closely approach those of *T. comorensis,* which also split into four flat segments and bear numerous stamens with long anthers, although flowers and buds of the latter are larger. Gynoecious flowers of *T. leptophylla* have acutely conical styles as in *T. kirkii* (Group 2B), but androecious flowers of the latter are much smaller, open only partially, and have fewer stamens (ca. 50) with short, medial loculi and acutely prolonged connectives. All three species are presumably derived from a common ancestor, perhaps one similar to *T. madagascariensis.*

Vernacular name. Ambora (Mayotte).

17. **Tambourissa kirkii** Cavaco, Kew Bull. 12(2): 228. 1957; Cavaco, Bull. Soc. Bot. France

104: 284, fig. 3. 1957. TYPE: Comore Archipelago. Johanna (Anjouan): without precise locality, Zambesi Expedition, 1,000 ft. (ca. 300 m), small tree, Aug. 1862 (fl, fr), *Kirk s.n.* (holotype, K) (see also Kirk's fig. 355, with type).

Monoecious shrub or small tree, the new growth hirsutulous, the mature leafy stems glabrous, stramineate, 2.5–4 mm diam. Leaves opposite to subopposite, glabrous, petiolate; petioles 10–15 mm by 1–1.5 mm; lamina ovate to elliptic, 100–135 mm by 55–70 mm, the apex shortly acuminate, the base obtuse to rounded, the secondary veins 6–7 pairs, making a 50–55° angle with the costa, the venation visible to 3–4° on both surfaces, the margin slightly revolute. Androecious inflorescence unknown. Androecious flower (from Kirk's fig. 355) globose, ca. 9–10 mm diam.; at anthesis deeply 3-fid, opening slightly, the lobes incurved; stamens probably ca. 50, subulate, ca. 3–4 mm long by 0.5 mm wide, the loculi separate, lateral, occupying medial ⅓ of stamen, the filament basally broad, comprising ca. ⅓ total length of the stamen. Gynoecious inflorescence a 4(–5)-flowered, finely velutinous pleiochasium, the position unknown, the floral axis ca. 20 mm by 1.5 mm, bearing rare, scattered bracteoles; female floral receptacle cupuliform-patelliform, 8–12 mm diam. by 5–6 mm long, the orifice broad, circular, entire, comprising ca. ¾ total width of the receptacle, the rim velutinous, the external surface finely velutinous, ± pustular; styles numerous, ca. 200, broadly conical, apiculate, 0.5–1 mm long by 0.5 mm diam. basally, bearing short, scattered hairs, the internal receptacle surface velutinous between the styles. Fruiting receptacle (from Kirk's fig. 355) broadly cupuliform-patelliform, ca. 250–300 mm diam., the broad, subcircular orifice comprising ca. ⅓–⅔ total width of the receptacle, the conical styles persistent in fruit. Mature (?) carpels ca. 10–12 mm long by 7–8 mm wide, ovoid-compressed, the endocarp "black and hard, surrounded with a red fleshy body" (fide Kirk).

Distribution. Endemic to Anjouan (Fig. 35).

Habitat. According to the information given on the label, *Tambourissa kirkii* occurs at 1,000 ft. (ca. 300 m), but on his figure 355 (an unpublished pencil drawing), Kirk notes "shrub growing at height of 2,000 feet (ca. 600 m) . . . seeds said to be cathartic. Monoecious." It probably occurs in montane wet forest.

Tambourissa kirkii belongs to species Group 2B. As noted by Cavaco (1957a), it is closely allied to *T. leptophylla* (Group 2A) from neighboring Mayotte. The latter differs by its more sparsely pubescent inflorescence, smaller gynoecious floral and fruiting receptacle orifice, glabrous styles, and by its androecious flower which is about twice as large with more numerous stamens having much longer loculi extending for almost the entire length of the stamen, and a scarcely prolonged connective.

Tambourissa paradoxa (Group 2B), also from Anjouan, has smaller, globular androecious flowers opening by a small pore and structurally similar stamens: it may even be conspecific with *T. kirkii.* As gynoecious flowers are unknown in the former, however, and androecious flowers of the latter are known only from a single pencil sketch, I have decided to recognize both species until further data and collections become available. *Tambourissa comorensis* and *T. leptophylla* differ by the characters mentioned above.

18. Tambourissa paradoxa Perk., Pflanzenr. 4, 101 (Nachtr.): 43. 1911. TYPE: Comore Archipelago. Johanna (Anjouan): without precise locality (fl), *Anon. sub Herb. Blackburn s.n.* (possibly *Bojer*) (holotype, K).

T. johannae Perk., Pflanzenr. 4, 101 (Nachtr.): 43. 1911. TYPE: Comore Archipelago. Johanna (Anjouan): Zylangi Lake, 27 Oct. 1862 (fl), *Anon. sub Zambesi-Expedition s.n.* (possibly *Kirk*) (holotype, K, lefthand specimen with flowers).

Monoecious shrub or small tree attaining 10 m tall, the new growth unknown, the adult leafy stems glabrous, terete, 3–4 mm diam., yellowish brown. Leaves opposite to subopposite, glabrous, petiolate; petioles 10–20 mm by 1–1.5 mm; lamina chartaceous, elliptic to ovate elliptic, 60–140 mm by 25–50 mm, the apex acute to acuminate, the base acutely cuneate to acutely decurrent, the secondary veins 5–8 pairs, making a 40–45° angle with the costa, the venation prominent and visible to 3° adaxially and to 4° abaxially, the margin moderately revolute. Androecious inflorescence ramiflorous, a sparse, puberulent pleiochasium of 3–11 flowers, or the flowers solitary and axillary, the floral axis 6–12 mm by 1 mm, bearing scattered, simple hairs, subtended by several pairs of minute, ciliate deltoid bracteoles. Androecious flower in bud globose, the pedicel 5–12 mm by 0.6–1 mm, bearing a few sparse hairs, subtended by 1(–2) minute, caducous deltoid bracteoles; at anthesis globose, 4–8 mm diam., not splitting but opening by a shallowly 4-lobed apical orifice ca. 2 mm diam. flanked by 4 small, decussate, obtusely deltoid ciliate tepals ca. 0.6–1 mm wide by 0.3–0.5 mm long, the internal surface of each lobe bearing 2–10 fleshy, obtuse to deltoid tepals intergrading with the stamens; stamens ca. 40–50, subulate-lanceolate, 2–3 mm long by 0.5–0.8 mm wide, the loculi lateral, separate, occupying basal ⅔ of stamen, the connective prolonged, acuminate, slightly exserted from the orifice at anthesis; internal receptacle surface glabrous. Gynoecious flowers unknown. Fruiting receptacle solitary on leafless branches, shallowly cupuliform, 53–150 mm diam. by 25–50 mm long, externally corky, the orifice comprising ca. ½ total width of receptacle, the internal surface with numerous broadly conical styles 0.7–0.8 mm long, more or less glabrous in between; pedicel and peduncle 15–17 mm by 5–7 mm. Mature carpels ovoid-compressed, 11 mm long by 6 mm wide.

Distribution. Endemic to Anjouan (Fig. 35).

Habitat. The species is apparently restricted to evergreen montane wet forest from ca. 650 to 1,400 m, according to available information.

ANJOUAN. WITHOUT PRECISE LOCALITY: Traprock (?) soils of hills, 2,000–3,000 ft., 29 Oct. 1862 (st), *Anon. sub Zambesi Expedition s.n.* (possibly *Kirk*) (K, sterile right hand specimen, not a type); (fl), *Levanché 21* (P); Oct. 1902 (fl, fr), *Levanché s.n.* (P); forêts, May 1850 (st), *Boivin s.n.* (P). N'TNIGUE PEAK: 4,200 ft. (ca. 1,400 m), in evergreen forest, food of pigeons, bulbuls and thrushes, tree ± 20 ft. tall with huge fruits hanging on stem filled with orange covered black seeds, 2 Oct. 1958 (fr), *Benson 142* (BM).

The types of *Tambourissa johannae* and *T. paradoxa* are both from Anjouan. Both collections have morphologically similar leaves, small, globular androecious flowers which open by a narrow apical orifice flanked internally by decussate, scale-like tepals, and have virtually identical stamens containing oil cells and a few sclerids, but lacking tanniferous idioblasts. It seems clear that these two concurrently published taxa are conspecific. I have chosen to retain the epithet *paradoxa,* as its type possesses more numerous and mature flowers than the type of *T. johannae. Tambourissa paradoxa* is an imperfectly known species and further field observations and collections, particularly of female flowers and fruit, are desired.

As is the case for *Tambourissa gracilis* and *T. purpurea* (both Madagascar), the androecious flowers of *T. paradoxa* open by small apical pores. Unlike the stamens of the former two, which are nearly sessile with apically confluent loculi, those of *T. paradoxa* are long and lanceolate with separate, lateral loculi and acute, prolonged connectives.

A close affinity appears to exist between *Tambourissa paradoxa* and *T. kirkii* (also Anjouan), which has strikingly similar floral and staminal morphology, although androecious flowers of the latter species split into 3–4 segments and lack the exserted connectives of the former. Both belong to species Group 2B. Similar androecious floral and staminal morphology occurs in *T. moheliensis* (Group 3) from neighboring Mohéli, although here the loculi are united basally into a U-shape, and the gynoecious flower differs in being closed in bud. The similarities in androecious floral and staminal morphology of *T. paradoxa, T. kirkii,* and *T. moheliensis* may be a result of convergence to accommodate similar pollinators, as the very different gynoecious flower of the latter suggests a closer affinity to the Madagascan *T. capuronii* (also Group 3).

Vernacular name. M'Bweza (Anjouan, fide *Benson 142,* BM).

19. Tambourissa moheliensis Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 300, pl. 2, figs. 9–11. 1982. TYPE: Comore Archipelago. Mohéli: mountains between Fomboni and Drodoni, low montane forest, 500–700 m, 6 Dec. 1967 (fl, fr), *Bernardi 11781* (holotype, Z; isotypes, G, K, P).

Monoecious or subdioecious tree 4–15 m tall by 70 cm diam., the new growth glabrous or with sparse, scattered hairs, the mature leafy stems pale green, terete, 2–5 mm diam. Leaves opposite to subopposite, glabrous, petiolate; petioles 7–22 mm by 1–1.5 mm; lamina subcoriaceous, ovate, broadly to narrowly elliptic, oblong or rarely obovate, 45–220 mm by 30–70 mm, the apex acute to acuminate, rarely rounded, the base acute to obtuse, cuneate or decurrent, rarely obtuse or rounded, the secondary veins 4–8 pairs, making a 45–65° angle with the costa, the venation visible to 2(–3°) adaxially and to 3(–4°) abaxially, the margin slightly revolute. Gynoecious inflorescence a finely pubescent, cauliflorous pleiochasium or thyrse of up to 20 flowers; androecious inflorescence a ramiflorous plei-

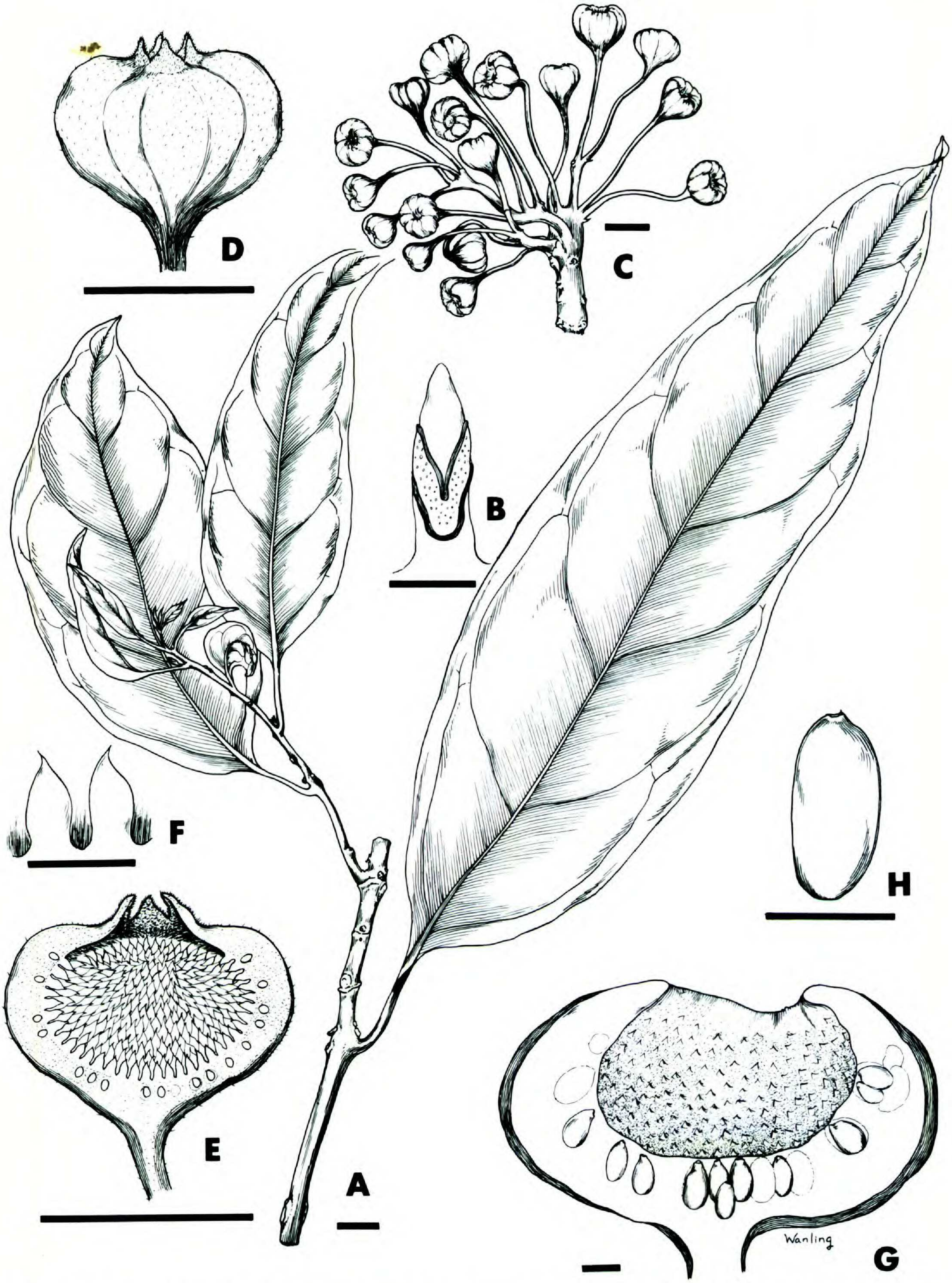

FIGURE 36. *Tambourissa moheliensis* Lorence.—A. Habit.—B. Stamen, adaxial view.—C. Submature gynoecious inflorescence.—D. Gynoecious flower at anthesis, lateral view.—E. Gynoecious flower, longitudinal section.—F. Styles, lateral view.—G. Submature fruiting receptacle, longitudinal section.—H. Fruiting carpel, lateral view. A–E. *Bernardi 11781* (G). F. *Bernardi 11759* (G). G, H. *Bernardi 11781* (Z). Bars equal 10 mm in A, C–E, G, H, and 1 mm in B, F.

ochasium of ca. 5 flowers on the leafless nodes, or the flowers solitary and axillary or rarely subterminal on short leafy shoots; floral axis 15–70 mm by 1–5 mm, finely pubescent or with scattered simple and fasciculate hairs, subtended by several ciliate-velutinous deltoid bracteoles. Androecious flower in bud globose, 4.5–6 mm diam., apiculate with 4 minute, decussate velutinous tepals, the pedicel 10–12 mm by 0.8 mm, bearing scattered hairs, subtended by a minute, deltoid caducous bracteole; at (complete?) anthesis globose, 5–6 mm diam., splitting into 4 shallow, inflexed lobes, each with 3–4 obtuse, scale-like tepals apically on the internal surface, these intergrading with the stamens, the internal receptacle surface glabrous; stamens ca. 50, narrowly acute to subulate, 2–2.5 mm long by 0.6–0.8 mm wide basally, the loculi subparallel, occupying ca. ⅔ total length of stamen, usually united basally into a single, U-shaped loculus, rarely free, the filament short, broad, the connective acute, prolonged. Gynoecious flower in bud napiform-depressed, pubescent, apiculate with 4 velutinous deltoid tepals 0.5 mm wide, the pedicels 20–40 mm by 1.5–2 mm, pubescent; at anthesis napiform-depressed, 12–16 mm diam. by 7–10 mm long, the orifice X-shaped, 1–2 mm wide, opening by 4 straight to suberect deltoid lobes, these finely pubescent-velutinous on both surfaces; styles numerous, ca. 100–200, conical, slightly ventricose medially, 1–1.3 mm long by 0.3–0.5 mm wide basally, glabrous, the internal receptacle surface velutinous with dense, simple and fasciculate hairs between the styles. Fruiting receptacle borne on the trunk, patelliform to napiform or subglobose, depressed, ca. 120 mm diam. by 70–75 mm long, the internal surface uniformly pale, corky gray-brown, the orifice comprising ca. ½ total width of receptacle, subentire, bearing remnants of the black, deltoid lobes, the walls ca. 20–26 mm thick, the internal surface bearing numerous scattered, narrowly conical, angular styles 1–1.5 mm long by 0.8–1 mm wide basally, interspersed with scattered to dense, simple and fasciculate hairs. Mature carpels ellipsoid to ovoid, compressed, 12–15 mm long, 6–7 mm wide, 4–5 mm thick, the endocarp dark brown, the surface scrobiculate. Figure 36.

Distribution. Endemic to Mohéli, Comores (Fig. 35).

Habitat. The species occurs in montane evergreen forest from ca. 500 to 700 m. Both flowers and fruits are produced in December.

MOHÉLI. FOMBONI: Bamboa, forest, 8 Mar. 1957 (fl), *Anon. in SF-16731* (P). MT. ST. ANTONIO: 600–700 m, in montane and submontane forest, 5 Dec. 1967 (fl, fr), *Bernardi 11759* (G, K, P, Z).

Mohéli, smallest of the four Comores, is probably also the most poorly explored botanically, with only three collections of *Tambourissa* known from the island. After much deliberation I have decided to treat all as a single species, although more extensive collections and field observations are required to ascertain whether or not they are truly conspecific.

The first collection, *Bernardi 11781*, possesses two gynoecious inflorescences with numerous flowers and a single submature fruit. Because it has numerous flowers in both thyrses and pleiochasia in addition to the fruit, I selected it as the type. *Anon. in SF-16731*, from the same locality, corresponds well with the type vegetatively, but the buds are unfortunately immature.

The third collection from Mohéli, *Bernardi 11759*, differs in having nearly glabrous new growth, smaller and more shortly acute or apically rounded leaves with fewer secondary veins oriented at a greater angle to the costa, and stronger, more distinct secondary vein arches. The more sparsely pubescent androecious flowers are in short, ramiflorous pleiochasia of up to five flowers, or rarely solitary and axillary or subterminal. Apart from the fact that the anther loculi are basally confluent in *Bernardi 11759* (Fig. 36B), the narrowly acute to subulate stamens with long connectives and closed, globular androecious flowers most closely resemble those of *T. kirkii* and *T. paradoxa* from nearby Anjouan, except that they contain dark tanniferous idioblasts. In terms of androecious floral and staminal morphology, *Bernardi 11759* could represent an undescribed species. The specimen at Geneva, however, has a single corky brown immature fruit with the orifice bearing six deltoid lobes that corresponds well with *Bernardi 11781*, and for this reason I tentatively consider them conspecific.

On the basis of androecious floral and staminal morphology, *Tambourissa moheliensis*, *T. kirkii*, and *T. paradoxa* would appear to be derived from a common ancestor. However, unlike the female receptacles of *T. kirkii*, *T. comorensis*, and *T. leptophylla* (all Group 2), which all have a circular, entire orifice open even in bud, that of *T. moheliensis* is closed in bud and splits open by four, deltoid segments as in *T. capuronii* (Madagascar). Moreover, the floral ground tissue of both the latter species contains numerous dark brown tanniferous idioblasts not found in the other Comorean species. These characters suggest that *T. moheliensis* was derived from a different ancestor than the other Comorean species and appears most closely allied to *T. capuronii* with which I have placed it in species Group 3.

Vernacular name. Diarou.

20. Tambourissa capuronii Cavaco, Bull. Mus. Hist. Nat. (Paris), Ser. 2, 29: 287. 1957; Cavaco in Humbert, Fl. Madagascar 80: 20, fig. VI:5–8. 1959. TYPE: Madagascar. Diego Suarez: Betsomanga Massif, valley on the S flank, ca. 550 m, 17 Nov. 1950 (fl), *Capuron 820-SF* (holotype, P; isotype, P).

Large monoecious tree 25–30 m tall and 40–60 cm D.B.H., the new growth hirtellous, the mature leafy stems glabrous, petiolate; petioles 12–30 mm by 1.2–1.5 mm; lamina chartaceous to subcoriaceous, abaxially hirtellous to glabrate, elliptic to oblong or obovate, (68–)90–165 mm by 30–74 mm, the apex shortly acuminate, acute or rarely obtuse, the base cuneate to acute, rarely obtuse, the secondary veins 7–10 pairs, making a 55–65° angle with the costa, the venation prominent, visible to 4° on both surfaces, the margin moderately revolute. Inflorescence a cauliflorous, unisexual or sexually mixed pleiochasium of 4–15 flowers, or rarely a fascicle of 2–3 flowers, all parts corky brown externally, the floral axis 10–170 mm by 1–5 mm. Androecious flower in bud globose, 15–19 mm diam., corky brown, slightly apiculate with coalescent tepals, the pedicel 28–55 mm by 2–2.5 mm; at anthesis deeply 4(–5)-fid, 40–55 mm diam., the lobes spreading flat; stamens numerous, ca. 300, lanceolate, 6–8 mm long by 1–1.5 mm wide basally, subsessile, the loculi narrow, separate, lateral, occupying the basal ¾–⅘ of stamen, the filament short or lacking, the connective acuminate, slightly prolonged, comprising apical ¼–⅕ of stamen, the apex sometimes bearing up to 5 simple hairs, the internal receptacle surface glabrous or with scattered simple hairs. Gynoecious flower in bud napiform-depressed, corky brown, 15–20 mm diam.; at anthesis to 35 mm long by 40 mm wide, the apex splitting into ca. 6 thick, irregularly deltoid lobes; styles numerous, ca. 200–300, narrowly conical, slender, 4–5 mm long by 0.5 mm wide basally, solitary or coalescent into groups of up to 12, the internal receptacle surface densely pilose between the styles and around the orifice; pedicel to 75 mm by 5 mm. Submature fruiting receptacle cupuliform, externally corky, 35 mm long by 55 mm diam., the carpels ovoid-compressed, to 13 mm by 8 mm.

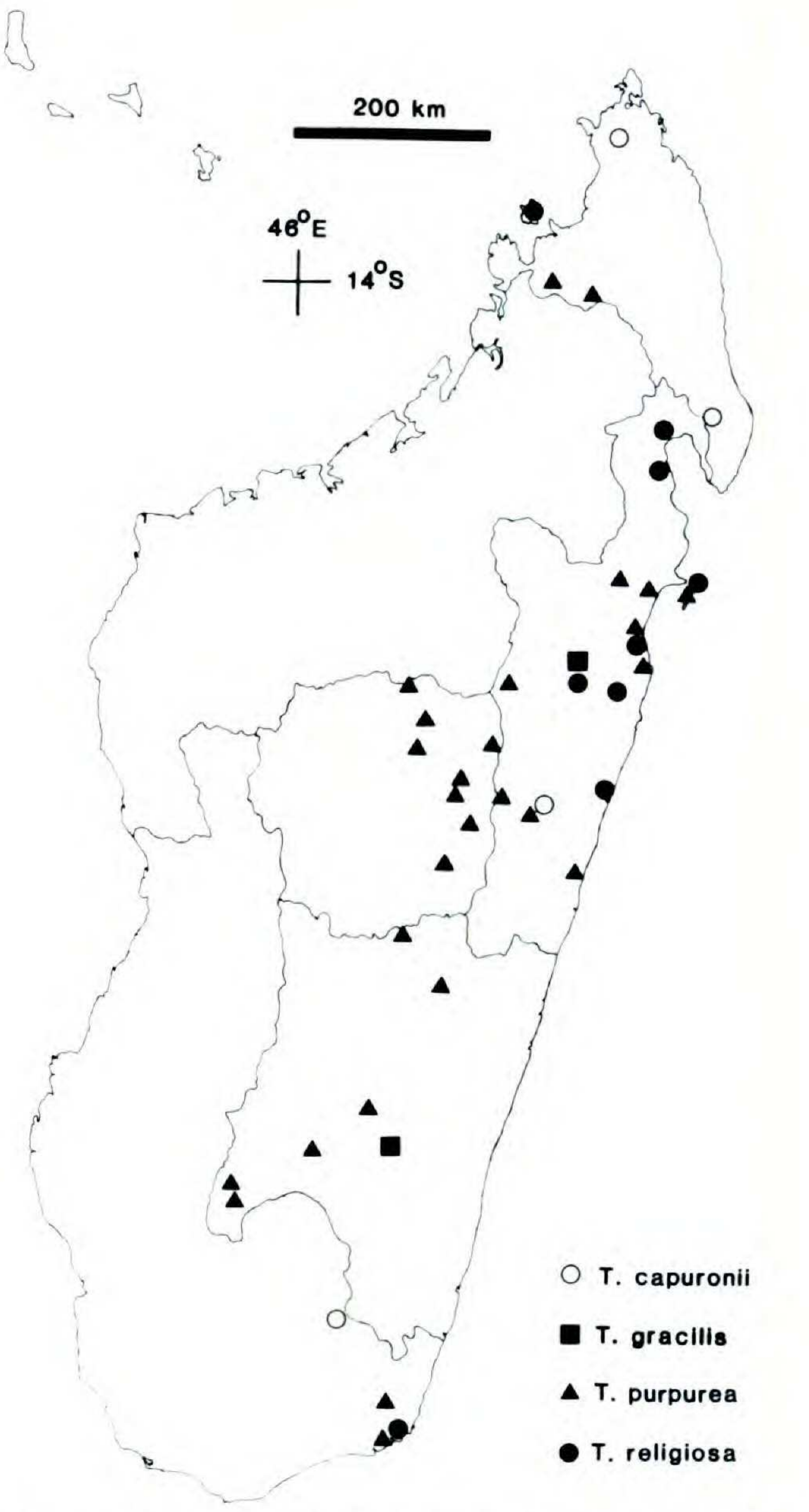

FIGURE 37. Distribution map of some *Tambourissa* species in Madagascar.

Distribution. Endemic to Madagascar (Fig. 37).

Habitat. Contrary to Cavaco's original (1957d) statement that the species was a highly restricted endemic, his subsequent list of exsiccata (1959) shows *Tambourissa capuronii* to be fairly widely distributed both in lowland Myristicaceae/*Anthostema* wet forest from ca. 300 to 800 m, and also in *Tambourissa*/*Weinmannia* montane wet forest from ca. 800 to 1,400 m, ranging from Mt. D'Ambre (Diego Suarez) in the north, south along the eastern escarpment, to the Mandrare River near Fort Dauphin in the southeast. The species was said by Capuron to be very abundant in 1950 at Betsomanga between 350 and 600 m. A canopy tree reaching ca. 30 m, it flowers in November–December and is one of the largest members of the genus.

MADAGASCAR. DIEGO SUAREZ: forêt d'Ambre, 1,200 m, Sept. 1926 (fl), *Perrier de la Bâthie 11741* (P). TAMATAVE: Analamazaotra forest (Perinet) 800 m (fl), *Perrier de la Bâthie 10087* (P); *Perrier de la Bâthie 10095* (P); Antasibe, Soanierana, E coast, 350 m, 10 Dec. 1938 (fl), *Lam & Meeuse 5835A* (P). TULEAR: upper basin of the Mandrare River (SE), pass and summit of Marosoui, forest on gneissic laterite, 1,000–1,400 m, 14–15 Nov. 1928 (fl), *Humbert 6606* (B, G, 2 sheets; K, MAD, P).

Tambourissa capuronii appears to be most closely related to the Comorean *T. moheliensis* with which it comprises species Group 3. The latter is distinguishable by its much smaller Androecious flowers and stamens, and styles which are never coalescent into groups as in *T. capuronii.* None of the other Madagascan species appears to be closely allied to *T. capuronii.*

21. **Tambourissa religiosa** (Tul.) A.DC., Prodr. 16(2): 659. 1868; Perk. & Gilg, Pflanzenr. 4, 101: 71. 1901; Drake in Grandidier, Hist. Phys. Madagascar 1(1): 23. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 44. 1911; Cavaco in Humbert, Fl. Madagascar 80: 36. 1959, excluding fig. X:5 (which is *T. elliptica* subsp. *micrantha*). *Ambora religiosa* Tul., Ann. Sci. Nat. (Paris) 4(3): 30. 1855; Tul., Monogr. Monim. 30, pl. XXVII. 1855. TYPE: "Bourbon" (Réunion). (Fide Richard, but probably Madagascar), ca. 1851 (fl), *Boivin s.n.* (lectotype, P, here designated).

Ambora tamburissa Boiv. ex Tul., Monogr. Monim. 303. 1855, non Lam. ex Steud.

Tambourissa boivinii A. DC., Prodr. 16(2): 659. 1868; Perk & Gilg, Pflanzenr. 4, 101: 70. 1901; Drake in Grandidier, Hist. Phys. Madagascar 1(1): 23. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911. TYPE: Madagascar. Tamatave: Sainte Marie Island, Lafondroa forest, Mar. 1847 (fr), *Boivin 1728* (holotype, P).

Tambourissa quadrifida sensu Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902, pro parte (as to *Baron 2504*), non Sonnerat.

Monoecious shrub, treelet, or small tree 4–5 m tall, the new growth glabrous, the mature leafy stems ascendant, dark brown to stramineate, 2.5–6 mm diam. Leaves opposite to subopposite, glabrous, petiolate; petioles (10–)15–30 mm by (1–)1.5–2.5 mm; lamina subcoriaceous to coriaceous, ovate elliptic, elliptic, oblong, narrowly oblong or obovate, 70–150(–175) mm by (16–)30–60 mm, the apex shortly acuminate, bluntly acute, obtuse or retuse, the base acute, cuneate or obtuse, often ± decurrent, the secondary veins 6–10 pairs, making a 60–70° angle with the costa, the venation obscure or visible to 2–3° adaxially, visible to 3–4° abaxially, the intramarginal loops uniting to form a conspicuous, partial marginal fimbrial vein, the margin thickened, moderately to strongly revolute. Inflorescence glabrous, either a terminal, axillary, or ramiflorous dichasium of 3 flowers or condensed pleiochasium of 5–7 flowers (the gynoecious flower terminal, if present), or the flowers solitary and terminal or axillary, the floral axis 1–7 mm by 1.5–2 mm, the axis and pedicels subtended by several glabrous to sparsely ciliate, broadly deltoid bracteoles with pale margins. Androecious flower in bud blackish to yellowish, globose to napiform, 7–10 mm diam. by 4–6 mm long, ± depressed, apiculate with 2–4 minute, deltoid glabrous tepals, the pedicel 3.5–5 mm by 1–1.5 mm; at anthesis unknown, presumably splitting into 4 shallow lobes (as in *T. purpurea*); stamens in bud ca. 60–82, linear-ellipsoid to slightly ovoid, 0.8–1 mm long by 0.5–0.7 mm wide, the filament short, distinct, slender, the loculi lateral, separate (rarely confluent apically), the connective rarely prolonged into an apicule, the internal surface with sparse hairs. Gynoecious flower in bud napiform-depressed, the pedicel 6–7 mm by 1–1.5 mm; at anthesis 8–11 mm diam. by 5–7 mm long, the orifice shallowly 4-lobed, X-shaped, 0.5–1.5 mm wide, the walls thick; styles numerous, ca. 300, conical, acuminate, slightly ventricose, 0.5–1.7 mm long by 0.3–1.5 mm wide basally, the internal receptacle surface with clusters of simple hairs between the styles. Fruiting receptacle terminal, solitary, or rarely paired, napiform-depressed to subglobose, to 52 mm diam. by 40 mm long, the external surface smooth, dark brown with corky patches, the orifice ca. 12 mm diam., comprising ¼–⅕ total width of receptacle, subcircular, subentire, the walls 10–17 mm thick, the internal surface with scattered conical-columnar styles 0.3–0.5 mm long and wide basally, interspersed with scattered hairs. Mature (?) carpels ovoid-compressed, 7–9 mm long, 5–6 mm wide, 4–5 mm thick, the endocarp light brown to beige, the surface shallowly scrobiculate.

Distribution. The species is endemic to Madagascar. Cordemoy (1895) erroneously cites the species as occurring in Réunion, but was actually referring to *Tambourissa crassa* (q.v.). The lectotype of *T. religiosa* was said by Richard to have come from Bourbon (Réunion), but this is undoubtedly due to a mixup in herbarium labels, because his other collections of the species are all from Madagascar and no other authentic specimens are known from Réunion (Fig. 37). It was selected because it represents the best of the four syntypes. The type of *T. boivinii,* although in poor condition, is clearly referable to *T. religiosa.*

Habitat. In Madagascar *Tambourissa religiosa* appears to be commonest in the eastern littoral forests where it occurs sympatrically with *T. purpurea.* The species ranges inland to the mountainous central plateau from altitudes of 1,500 to 1,700 m, and across the northwestern region to the offshore island of Nosy Be.

MADAGASCAR. DIEGO SUAREZ: Nossi Be, 23 July 1840 (st), *Pervillé 295* (P, syntype); 10 Oct. 1840 (fr), *Pervillé 328* (P, syntype). TAMATAVE: Ambila, 1 May 1928 (fl), *Decary 6288* (MAD, P); 10 May 1928 (fl, fr), *Decary 6554* (K, MAD, P); Rantabe, N of Tamatave, littoral forest, 1 June 1969 (st), *Guillaumet 3002 bis* (MAD); Maroa, forests within Antongil Bay, 1867 (fl), *Moquerys 66* (G, Z); Reserve no. 1, Tamatave, 21 June 1950 (fl), *Rakotoniama sub RN 3956* (MAD, 2 sheets); Sainte Marie Island (East Coast), Sept. 1851 (fl), *Boivin s.n.* (P, syntype); (fl), *Boivin s.n.* (P, syntype); Mar. 1847 (fr), *Boivin 1728* (P, holotype of *T. boivinii*); Ambila, Lemaitsoa, littoral forest, Aug. 1975 (fl, fr), *Rakotozafy 1293* (MAD); Androndramanika, Rahobevava, 830 m (near Lac Alaoatra), 10 May 1951 (fr), *Cours sub Herb. Alaotra 4270* (MAD). WITHOUT PRECISE LOCALITY: Central Madagascar, 1883 (fl), *Baron 2499* (K); (fl), *Baron 2504* (K); Dec. 1883 (fl), *Baron 2766* (K, 2 sheets); East Coast, Mar. 1891 (fr), *Baron 6043* (K); 1865 (fl), *Gerrard 35* (K); 1883 (fl), *Humbolt 190* (K).

Tambourissa religiosa belongs to species Group 4 and appears to be most closely allied to *T. purpurea,* another Madagascan species with structurally similar leaves and flowers. Observations on living material of *T. religiosa,* however, are required to ascertain whether or not its gynoecious flowers produce a mucilaginous "hyperstigma" as do those of *T. purpurea* (studied by Endress, 1979 and 1980b, as *T. religiosa*). Ripe fruiting receptacles of both species are smooth and reddish as opposed to those of most congeners which are pale brown and corky.

Tambourissa religiosa is distinguishable from *T. purpurea* by its floral receptacles which are more than twice as large, its more numerous stamens with separate loculi and distinct filaments, its more numerous, acute styles, and by its larger, more coriaceous leaves with a thicker hypodermis, prominent partial marginal fimbrial vein, and revolute margins.

Vernacular names. Ambora, Laingafora (Madagascar). According to Commerson, certain Malagasy tribes used *Tambourissa religiosa* in a religious context, burying their dead with its branches.

22. Tambourissa purpurea (Tul.) A.DC., Prodr. 16(2): 659. 1868; Perk. & Gilg, Pflanzenr. 4, 101: 69, fig. 18:5. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911; Cavaco in Humbert, Fl. Madagascar 80: 39, fig. V:1. 1959. *Ambora purpurea* Tul., Ann. Sci. Nat. (Paris) 4(3): 30. 1855; Tul., Monogr. Monim. 301, pl. XXVI. 1855. TYPE: Madagascar. Tamatave: Sainte Marie Island (ca. 1850) (fl, fr), *Bernier 262* (lectotype, P, here designated; isolectotype, P).

Tambourissa rota Baker, J. Linn. Soc., Bot. 20(128): 240. 1883; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911; Perk., Gatt. Monim. fig. 34:5. 1925; Cavaco in Humbert, Fl. Madagascar 80: 38, fig. X:6. 1959. TYPE: Madagascar. Central Madagascar: without precise locality (ca. 1881) (fl, fr), *Baron 764* (lectotype, K, here designated; isolectotype, P).

T. quadrifida sensu Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902, pro parte, non Sonn.

T. rota var. *longipetiolata* Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911. TYPE: Madagascar. Central Madagascar: without precise locality (fr), *Baron 1642* (holotype, K).

Monoecious shrub, treelet, or small tree attaining 10 m tall and 30–40 cm D.B.H., the bark gray-black, longitudinally fissured, the branches often decumbent and trailing, the new growth glabrous or with rare, scattered hairs, the mature leafy stems brownish, 2–3 mm diam., terete. Leaves opposite to subopposite, rarely ternate on vigorous sucker shoots, glabrous, petiolate; petioles 3–10(–17) mm by 0.8–1.3 mm, red to purple when living; lamina chartaceous to subcoriaceous, ovate-elliptic, elliptic, oblong, narrowly oblong or obovate, (25–)40–85(–100) mm by (10–)15–40(–44) mm, the apex acuminate, acute, obtuse or retuse, the base cuneate, acute, obtuse, truncate or even subcordate, often ± decurrent, the secondary veins 4–11 pairs, making a 60–70° angle with the costa, the venation visible to 2–4° or obscure adaxially, visible to 2–3° abaxially, the margin plane to slightly revolute. Inflorescence ramiflorous, axillary, or terminal on leafy shoots, a 3-flowered dichasium or a contracted pleiochasium of 5 flowers (the gynoecious flower terminal, if present), or the flowers solitary, or in sparse fascicles on old stems, the floral axis

1–4 mm by 1 mm, glabrous to puberulent, the axis and pedicels subtended by 1 to several ciliate to hirsute, naviculate bracteoles. Androecious flower in bud sparsely pubescent to glabrous, globose-depressed to napiform-depressed, 2–3(–4) mm diam. by 2.5–3.5(–4) mm long, the apex with 1–3 pairs of minute, acute to rounded ciliate tepals, the pedicel 2.5–6(–10) mm by 0.6–1 mm; at anthesis 2.5–3.5 mm diam., shallowly (3–)4-fid for up to $\frac{1}{2}$ its length, the lobes incurved or spreading slightly, the orifice 1–3 mm diam.; stamens 20–32, acutely deltoid to obtusely deltoid, 0.7–1.2 mm long by 0.6–1 mm wide, the loculi confluent apically into a single, crescentiform loculus, the filament very short or sessile, the internal receptacle surface glabrous or with rare, scattered hairs. Gynoecious flower in bud globose-depressed to napiform-depressed, glabrous to sparsely pubescent, apiculate with 2–3 pairs of minute tepals, the pedicel 5–6 mm by 1 mm; at anthesis urceolate-globose to urceolate-napiform, 4(–7) mm diam. by 4(–7) mm long, the orifice 3–4-lobed, 0.5–1 mm diam., when living occluded by a mucilaginous plug, the inner tepals stigmatic; styles 35–70(–90), shortly columnar, apiculate, 0.3–0.4 mm long by 0.2–0.3 mm diam., the internal receptacle surface glabrous or with rare, scattered hairs between the styles. Fruiting receptacle terminal, solitary, globose-urceolate, ± depressed, 28–50 mm diam. by 25–40 mm long, the external surface dark reddish brown to blackish, occasionally mottled with pale gray-brown, corky patches, the orifice subentire, ± circular, 2–7 mm diam., comprising $\frac{1}{10}$–$\frac{1}{6}$ total width of the receptacle, the walls 8–11 mm thick, the internal surface with scattered, subcircular styles ca. 0.5 mm diam., glabrous or with rare, scattered hairs. Mature carpels ovoid-compressed, 6–9 mm long, 4–7 mm wide, 3.5–5 mm thick, the endocarp brown, the surface scrobiculate to reticulate-foveate. Gametic chromosome number, $n = 19$.

Distribution. Endemic to Madagascar (Fig. 37).

Habitat. *Tambourissa purpurea* is one of the most widely distributed members of the genus in Madagascar, along with *T. hildebrandtii* and *T. religiosa.* Quite variable vegetatively, it displays a wide ecological amplitude ranging from littoral forest along the east coast, through the lowland and submontane wet forest zones of the eastern escarpment (up to ca. 1,400 m), and into montane forest of the central plateau (ca. 1,400–1,600 m). It also extends westward into the semi-deciduous dry forest zone of the western sector as far as the Isalo massif, where it is apparently able to survive annual burning, taking on a shrubby habit with numerous erect coppice shoots.

In living plants, floral receptacles of *Tambourissa purpurea* range from green to dark reddish purple. The gynoecious flowers produce a mucilaginous plug or "hyperstigma" (see Endress, 1979, 1980b) that is probably functional in pollination. Androecious flowers of *Lorence 1725* (MO) produced a faint sweet, almost musky, odor.

MADAGASCAR. FIANARANTSOA: Isalo, 13 Apr. 1961 (fl), *Anon. sub Herb. Peltier 3044* (MAD); Ihosy, Mont Lalandro, 1,100–1,200 m, 5 Nov. 1967 (fr), *Bernardi 11230* (K); Route no. 7, 39 km N of Ambositra, 1,250–1,350 m, 24 Jan. 1975 (fr), *Croat 29458* (MAD, MO); 10 km W of Ivato on Route 35, 1,365 m, 25 Jan. 1975 (fr), *Croat 29545* (MAD, MO); Massif d'Isalo, 10 km W of Ranohira, Route 7, 810 m, 3 Feb. 1975 (fl), *Croat 30568* (MAD, MO); Ambohimitombo forest (Fanala), 1,350–1,440 m, 4 Jan. 1895 (fl), *Forsyth Major 328* (K); (fl), *Forsyth Major 340* (K); 21 Jan. 1895 (fr), *Forsyth Major 710* (K); Betsileo Land, 1880 (fr), *Langley Kitching s.n.* (K); National Route no. 7 at 11 km W of Ambalavao, 950 m, 5 Nov. 1978 (fl), *Lorence 2042b* (K, MAD, MAU, MO, P, Z); (fl), *Lorence 2044* (K, MAD, MO, Z); National Route no. 7 at 9 km SW of Ranohira (Isalo), 800 m, 6 Nov. 1978 (fr), *Lorence 2058* (MAD, MO); (fr), *Lorence 2059* (MAD, MO); (st), *Lorence 2060* (MAD, MO). MAJUNGA: Natural Reserve no. 4, Marovato, Ambanja, 10 July 1952 (fr), *Safy sub RN 4180* (MAD, 2 sheets). TAMATAVE: Soanierana, Ivongo (near Sainte Marie Island), 27 Dec. 1949 (fr), *Anon. sub SF 2346* (MAD); Anjahana, Foule Pointe, 12 June 1950 (fr), *Anon. sub SF 2585* (MAD); Natural Reserve no. 3, Sahatavy, Fenoarive, 17 June 1952 (fl), *Anon. sub RN 4137* (MAD); Vohimaranitra, Tamatave, 26 Jan. 1951 (fr), *Anon. sub RN 1989* (MAD); Sainte Marie Island, Tafondron Forest, Mar. 1847 (fl, fr), *Boivin 1729* (P, syntype, 2 sheets); Morarano, pseudosteppes on dry slopes (W of Lac Alaotra), Dec. 1954 (fl), *Bosser 7502* (MAD); on sand between Mahanoro and Vatomandry, 2 July 1972 (fr), *Cremers 2310* (MAD, 2 sheets); Ambila, littoral forest, 8 May 1928 (fr), *Decary 6450* (P); Fenoarivo, 18 Mar. 1930 (fl), *Decary 7633* (MAD); National Route no. 2 at 89 km E of Tananarive, Mandraka Forest, 1,400 m, 30 Oct. 1978 (st), *Lorence 2036* (MAD, MO); Perinet, 70 km E of Tananarive (cultivated in Heidelberg Bot. Garden) Oct. 1976 (fl), *Rauh M 138* (Z). TANANARIVE: Analabe, Anjozorobe, Mar. 1953 (fr), *Bosser 5219* (MAD, 2 sheets); Tampoketsa, Ankazobe, Pk 120, road to Majunga, Apr. 1955 (fr), *Bosser 7855* (MAD); Andramasina, Ambatolampy (fl, fr), *Bosser 12466* (MAD, 2 sheets); forest at Pk 142 along the road from Tananarive to Majunga, 8 July 1971 (fr), *Cremers 1641* (MAD); Tananarive, Tsimbazaza Park, 1,200 m, 17 Jan. 1975 (fl), *Croat 28636* (MAD, MO); near Tananarive, 28 July 1928 (fr), *Decary 6610* (MAD); Tananarive, Tsimbazaza Park, cultivated in back of Philippe Morat's house (originally from Perinet), 28 May 1974, *Gentry & Morat 11964* (MAD, MO); forests of Tampoketsa, May 1956 (fr), *Rialinansy 1027* (MAD); bottom of the valley Ambohimanga south, 9 Nov. 1963 (st), *Rakotozafy 204* (MAD); "tapias" (*Uapaca* forest), Pk 36, road to Antsirabe, 16 Feb. 1966 (fl), *Rakotozafy 460* (MAD); Vakinankaratra, Ambatolampy, banks of the Onive River, near Tsinjoarivo, 1,600 m, 1 Dec. 1912 (fr), *Viguier & Humbert 1913* (G). TULEAR: along road through mountain forest in Chaines Anosyennes from Fort Dauphin to Ranamafona, 40–60 m, 1–28 km from Route no. 10, 19 Feb. 1975 (fr), *Croat 31778* (MAD, MO); (fr), *Croat 31779* (MAD, MO); dunes, Fort Dauphin (fr), *Pernet sub Herb. Inst. Sci. Madagascar 29* (MAD); Fort Dauphin (fl), *Rauh 1440* (MAD). PROVINCE UNCERTAIN: Amtranokofa, Natural Reserve, 8 July 1950 (fr), *Anon. sub SF 43* (MAD); forest N of the road to Nickaville, 29 Dec. 1944 (st), *Anon. sub Herb. Alaotra 2081* (MAD); Antsahabe to Antsakalalina, 20–40 m, 5 Apr. 1949 (fr), *Anon. sub Herb. Alaotra 3607* (MAD); Andrangoalaka, Central Madagascar, 1881 (fr), *Baron s.n.* (K); 1882 (fl), *Baron 1239* (K, syntype of *T. rota*); (st), *Parker s.n.* (K); Central Majakotompo, Nov. 1955 (fr), *Bosser 8709* (MAD); Antongona, rocks, Jan. 1960 (fl), *Bosser 13509* (MAD); Pk 44, road to Majunga, Mar. 1963 (fr), *Bosser 17192* (MAD); valley of the Saonjo, May 1964 (fr), *Morat 1140* (MAD); Antongona, 16 Jan. 1960 (fl), *Peltier 1763* (MAD); Maroamalona, Rankafina, 14 Nov. 1963 (fr), *Rakotozafy 228* (MAD); Tsaravinany, Apr. 1966 (fr), *Rakotozafy 588* (MAD). WITHOUT PRECISE LOCALITY: 1881 (fl, fr), *Baron 790* (K, P, syntypes of *T. rota*); 1882 (fl), *Baron 1361* (K, P, syntypes of *T. rota*); (fr), *Baron 2996* (K); 1883 (fr), *Baron 3024* (K, P); 1885 (fr), *Baron 3515* (K, P); (st), *Baron 3575* (BM); (fr), *Baron 4241* (K, P); (fr), *Baron 4325* (K); 1892 (st), *Baron 6675* (BM); (st), *Parker s.n.* (K); North Madagascar, 1892 (fr), *Baron 6439* (K). CULTIVATED: Missouri Botanical Garden, grown from wild seed obtained from Madagascar, 23 June 1977 (fl), *Lorence 1725* (MO); (fl), *Lorence 1726* (MO); 13 Feb. 1980 (fl), *Lorence 2954* (MO).

Although *Tambourissa purpurea* is extremely variable in terms of foliar morphology, even on a single individual (e.g., *Croat 29458*, MO), its flowers are quite constant and the smallest in the genus. Along with *T. gracilis* and *T. religiosa*, it belongs to species Group 4. Flowers of *T. religiosa*, however, are about twice as large as those of *T. purpurea*, have more numerous parts, and the leaves are thicker with a well-developed hypodermis of (3–)5–6 cell layers comprising ca. ⅓–½ of the total laminar thickness. That of *T. purpurea* is only (1–)2–3 cell layers thick and comprises only ⅙–⅓ of the total laminar thickness. Also, *T. purpurea* lacks the prominent partial marginal fimbrial vein of the former species. Both occur sympatrically in eastern and central Madagascar and no hybrids or intermediates are known to occur.

Tambourissa purpurea is perhaps even more closely allied to *T. gracilis* in terms of foliar and androecious floral morphology (gynoecious flowers are unknown in the latter). The pleiochasia are much laxer in *T. gracilis*, however, with a much longer floral axis and pedicels.

Vernacular names. Ambora, Ambora vavy, Rota, Villainque-possa (Madagascar).

23. **Tambourissa gracilis** Perk., Pflanzenr. 4, 101 (Nachtr.): 43. 1911; Cavaco in Humbert, Fl. Madagascar 80: 35. 1959. TYPE: "Central Madagascar." Without precise locality (probably Tananarive or Fianarantsoa): ca. 1888 (fl), *Baron 2885* (holotype, K; isotype, P).

T. leptophylla sensu Drake in Grandidier, Hist. Phys. Madagascar 1(1): 23. 1902 non (Tul.) A.DC.

Dioecious (?) treelet or small tree 8–10 m, the mature leafy stems glabrous, 1.5–2.5 mm diam. Leaves opposite, glabrous, petiolate; petioles 14–17 mm by 1 mm; lamina chartaceous, elliptic or rarely oblong, 75–120 mm by 26–45 mm, the apex long acuminate, the base acutely cuneate, decurrent, the secondary veins 6–9 pairs, making a 65–85° angle with the costa, the venation raised and visible to 4° on both surfaces, the margin plane to slightly revolute. Androecious inflorescence ramiflorous on leafless nodes or axillary, a unisexual pleiochasium of 3–7 flowers, sparsely pubescent with pale, appressed hairs, the floral axis 7–25 mm by 1 mm, subtended by several basal bracteoles. Androecious flower in bud globose, 6–8 mm diam., apiculate with a pair of semicircular, obtuse tepals, the pedicel 5–13 mm by 1 mm, subtended by 1(–2) hirsute, naviculate bracteoles 1–2 mm long; at (full?) anthesis globose, 6–8 mm diam., the subcircular orifice 1–2 mm diam., occasionally splitting slightly, flanked internally by several pairs of obtuse, scale-like tepals; stamens ca. 50, broadly deltoid, 1.2–1.7 mm long by 1 mm wide, the loculi occupying almost entire length of the stamen, confluent apically into a single, crescentiform loculus, the filament very short or sessile, the internal receptacle surface with rare, scattered hairs. Gynoecious inflorescence unknown. Submature fruiting receptacles borne in clusters of 2–3, shallowly cupuliform, 30–55 mm wide by 20–30 mm long, the orifice comprising ⅔–¾ total width of fruit, the styles conical, 0.6–0.8 mm long; fruiting carpels ovoid-compressed, 9–10 mm long by 7–8 mm wide, tan.

Distribution. Endemic to Madagascar (Fig. 37).

Habitat. According to Humbert (1965) and Cavaco (1959), *Tambourissa gracilis* occurs in high altitude ericoid heath formation (ca. 1,800–2,700 m) on mountains of the central plateau and vicinity. However, a fruiting specimen (*Humbert 3688,* P) named by him and cited by Cavaco (1959) is closer to *T. purpurea,* from which it differs in having disorganized venation characteristic of neither species. As the specimen lacks flowers, a more complete analysis is impossible.

MADAGASCAR. DIEGO SUAREZ: Tsaratanana Massif, 1,400 m, Nov. 1912 (fr), *Perrier de la Bâthie 10105* (P).

Tambourissa gracilis belongs to species Group 4. With respect to its androecious flowers, which have short, subsessile stamens and apically confluent loculi, it appears to be most closely related to *T. purpurea* which differs in having a shorter floral axis and pedicels. Foliar morphology of the two species is virtually identical, also resembling that of *T. madagascariensis* (Group 2A). Further collections of this imperfectly known species, especially gynoecious flowers and fruits, are needed to better understand its affinities.

24. Tambourissa pedicellata Baker, Fl. Mauritius 289. 1877; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911; Vaughan, Mauritius Inst. Bull. 1(1): 76. 1937. TYPE: Mauritius. Without precise locality; in the shade of humid forests, on the high mountains, 1864 (fl, fr), *Bouton s.n.* (lectotype, K).

Ambora amplifolia sensu Tul., Monogr. Monim. 299. 1855, pro parte, non Boj. ex Tul.
Tambourissa amplifolia sensu A.DC., Prodr. 16(2): 659. 1868, pro parte; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901, pro parte, non (Boj. ex Tul.) A.DC.

Monoecious tree attaining 15 m tall and 30 cm D.B.H., the crown compact, the bark pale brown, smooth, flaking, the new growth sparsely puberulent, glabrescent, the mature leafy stems 2.5–6 mm diam., terete, the nodes dialated. Leaves opposite, rarely subopposite, glabrous, petiolate; petioles (2–)6–13 mm by 1.5–3 mm; lamina chartaceous to coriaceous, elliptic to narrowly elliptic or oblong, rarely broadly elliptic to suborbiculate, (30–)50–160(–200) mm by (15–)22–80(–120) mm, the apex acuminate, acute, obtuse, rounded or retuse, the base acutely decurrent to acutely cuneate, the secondary veins 5–12 pairs, making a 50–65° angle with the costa, the venation obscure adaxially and visible to 2(–3°), dark brown abaxially and visible to 3(–4°), the margin slightly thickened, moderately revolute. Inflorescence a glabrous, ramiflorous (rarely terminal), leafless or leafy, unisexual or sexually mixed pleiochasium of 5–14 flowers, or a cauliflorous, leafy or leafless pleiochasium or rarely dichasium, the floral axis (15–)35–200 mm by 1.5–4 mm, often ± flattened, frequently subtended by several deltoid-naviculate puberulent bracteoles; flowers monomorphic. Androecious flower in bud napiform-depressed, 7–11 mm diam. by 4–7 mm long, externally smooth with scattered hairs, the apex with 4 minute, puberulent tepals, the pedicel long, slender, 15–66 mm by 0.7–1.5 mm, subtended by a single puberulent, subulate-deltoid bracteole 1–2 mm long or by a small leaf; at anthesis shallowly 4–6-fid, subglobose, 10–14 mm diam., the lobes thick, short, acuminate, incurved to erect, the orifice comprising ½–⅔ total width of the receptacle; stamens 50–70, minute, deltoid to ellipsoid, 0.6–1 mm long by 0.5–0.8 mm wide, the loculi short, broad, subparallel, separate or occasionally confluent apically, sometimes ± unilateral, occupying ⅔–¾ total length of the stamen, the filament short, basally ventricose, the connective not prolonged, the internal receptacle surface glabrous. Gynoecious flower in bud subglobose to napiform-depressed, 8–10 mm diam. by 5–7 mm long, externally smooth with scattered hairs, the apex with 3–4 minute, puberulent tepals, the pedicel as in the androecious flower; at anthesis shallowly 4–7-fid, subglobose, 6–12 mm diam. by 5–7 mm long, the lobes thick, acute to acuminate, erect, the orifice subentire, comprising ca. ½–⅔ total width of the receptacle, the walls thick; styles ca. 60–180, conical, 0.8–1.2 mm long by 0.3–0.4 mm wide basally, the apex slightly papillose, the base ventricose, the internal receptacle surface glabrous or with sparse clusters of hairs between the styles. Fruiting receptacle produced on the branches, solitary or in a leafy pleiochasium of up to 5 fruits, ± subglobose, 18–32 mm diam. by 12–25 mm long, the orifice small, shallow, comprising ca. ¼–½ total width of the receptacle, the rim subentire, thickened, with persistent deltoid lobes, the external surface mottled, pale corky brown with darker patches,

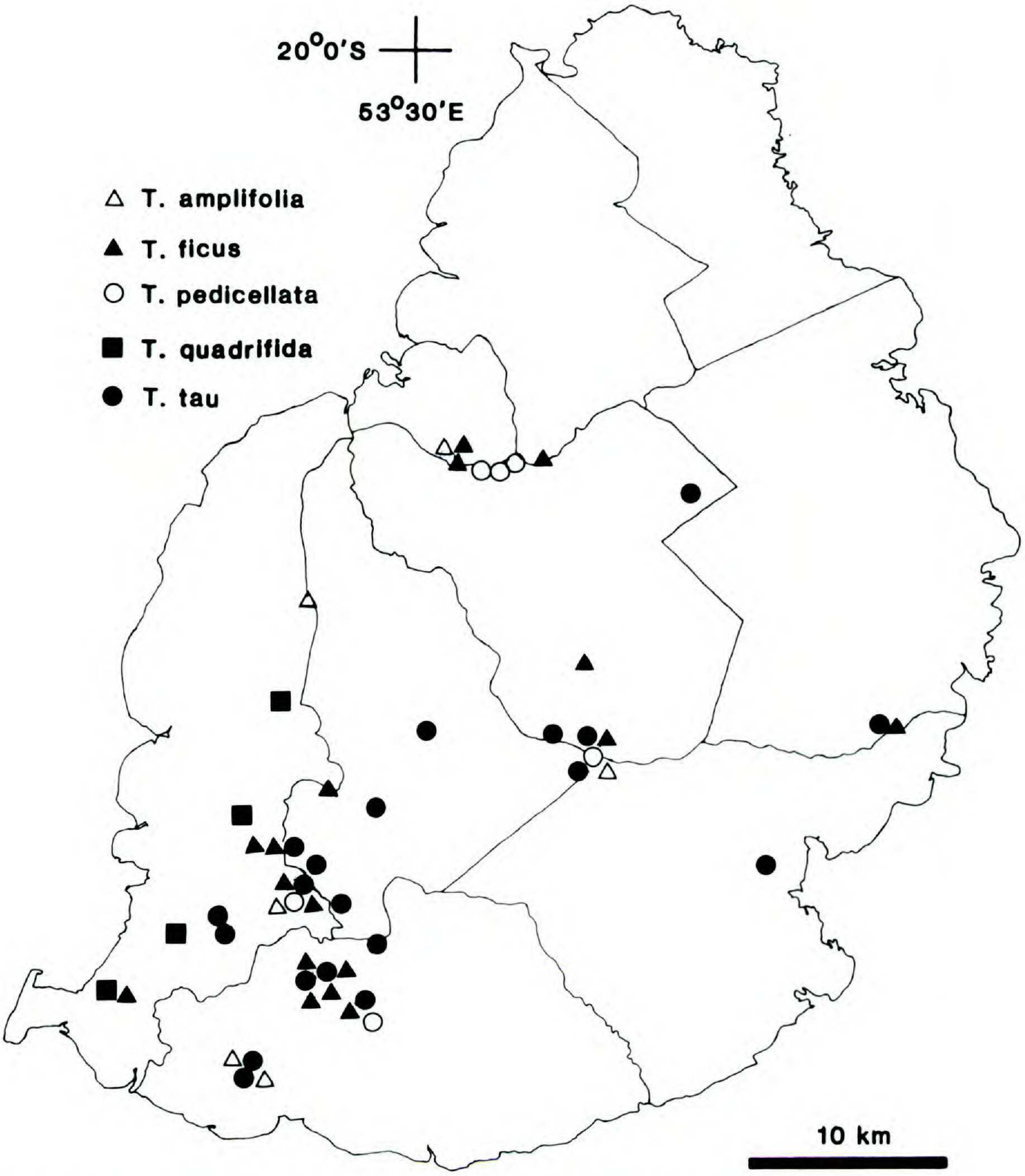

FIGURE 38. Distribution map of some *Tambourissa* species in Mauritius.

the cavity small, the numerous styles conical, 0.6–1 mm long by 0.4–0.7 mm diam. basally, interspersed with rare, scattered hairs, the pedicel slender, 20–55 mm by 1.5–2.5 mm. Mature carpels ovoid-compressed, 8–11 mm long, 6–8 mm wide, 4–6 mm thick, the endocarp dark brown with 1 to several longitudinal, ± branching ridges, the surface foveate-scrobiculate. Gametic chromosome number, $n = 19$.

Distribution. The species is endemic to Mauritius (Fig. 38).

Habitat. *Tambourissa pedicellata* is presently known only from four localities in wet and cloud forest: the southern flank of the Pieter Both mountain range, where I estimate the total population to consist of 50 to 100 individuals; at Mt. Lagrave, where a small population occurs in cloud forest near the summit; in Bassin Blanc crater, where a single individual was located. Vaughan and Wiehe (1941) recorded *T. pedicellata* from Macabé forest (*Vaughan 1327 sub MAU 2358,* MAU), but I was unable to relocate it there during extensive searches made in 1974–1977 and again in 1978–1979. In 1983, W. Strahm (pers. comm.) located an "individual" of *T. pedicellata* at Macabé whose trunk was fused with that of *T. sieberi* in what apparently represents a perfect natural graft.

My observations on the Pieter Both population during the course of a year showed the plants to be evergreen and not deciduous as stated by Vaughan and Wiehe (1941). Most individuals here flowered from February through April 1979, although one tree was flowering in November 1978. Fruits generally ripened in February. Living flowers of *T. pedicellata* produce little apparent odor, although a faint, fruity smell was detected in some. Buds and receptacles are mottled green externally, and the stamens may be cream, yellow, or yellowish pink, whereas the styles range from bright orange to reddish orange.

MAURITIUS. BASSIN BLANC CRATER: wet forest near lake, ca. 500 m, 6 July 1979 (st), *Lorence 2967* (MO). MACABÉ FOREST: Macabé transect (symbol T_2) 16 June 1937 (st), *Vaughan 1327 sub MAU 2358* (MAU). MT. LAGRAVE: S slope facing Eau Bleue reservoir, near summit, ca. 600–628 m, 24 May 1979 (st), *Lorence 2966* (MO). PIETER BOTH MOUNTAIN RANGE: S flank, 500–600 m, 29 Nov. 1978 (fl), *Lorence 1834* (K, MAU, MO, 2 sheets; P); 13 Feb. 1979 (fl), *Lorence 2384* (K, MAU, MO, 2 sheets; Z); (fl, fr), *Lorence 2385* (B, G, K, MAU, MO); (fl, fr), *Lorence 2386* (K, MAU, MO, P, REU); 19 Apr. 1979 (fl), *Lorence 2598* (MAU, MO); (fl), *Lorence 2599* (MAU, MO). QUARTIERE MILITAIRE: 1863 (fl), *Anon. sub Herb. Blackburn s.n.* (K, syntype, 2 sheets). WITHOUT PRECISE LOCALITY: (fl, fr), *Anon. sub Herb. Richard s.n.* (P); (fl), *Anon. sub MAU 1311* (MAU); 1814 (fl, fr), *Carmichael s.n.* (K); ca. 1755 (fl), *Commerson s.n.* (P); (st), *Anon. sub Herb. Ventenat s.n.* (G, 2 sheets).

In terms of floral morphology, *Tambourissa pedicellata* appears to be one of the least specialized species in Mauritius and possibly in the entire genus. It appears to fit best in species Group 5, however. Among Mauritian species, *T. pedicellata* is most similar to *T. amplifolia* which also has long, slender floral pedicels, small subglobose buds and receptacles, and small stamens and styles; the two species have been confused in the past (De Candolle, 1868; Perkins & Gilg, 1901). *Tambourissa amplifolia* is readily distinguishable, however, by its smaller, more slender habit, basal cauliflory, much larger leaves, discoid gynoecious flowers with everted lobes, and androecious flowers deeply split into four flat lobes bearing stamens with apically confluent loculi.

Although *Tambourissa purpurea* (Madagascar) also has monomorphic androecious and gynoecious flowers, it appears to represent a highly specialized condition because of the mucilaginous "hyperstigma" of the gynoecious flowers (see Endress, 1979, 1980b; as *T. religiosa*). The majority of Mauritian species with opposite leaves, more or less open, cupuliform to napiform or globose gynoecious flowers and conical to setose styles also belonging to Group 5 may have been derived from a common ancestor which *T. pedicellata* most closely approaches today.

25. **Tambourissa amplifolia** (Bojer ex Tul.) A.DC., Prodr. 16(2): 659. 1868; Baker, Fl. Mauritius 287. 1877; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901, pro parte; Perk., Pflanzenr. 4, 101 (Nachtr.): 43. 1911. *Mithridatea amplifolia* Bojer, Hortus Maurit. 290. 1837 nom. nud. *Ambora amplifolia* Bojer ex Tul., Monogr. Monim. 299. 1855. TYPE: Mauritius. Woods of Grand Port: Pouce Mountain, Aug. 1851, *Boivin s.n.* (holotype, P).

Monoecious understory treelet or small tree attaining 8 m tall and 9 cm D.B.H., sometimes shrubby, the branches few, erect, the new growth sparsely hirsutulous, the leafy stems terete, 5–14 mm diam., glabrous, the nodes dialated. Leaves often clustered near the ends of the branches, opposite to subopposite, sometimes congested into pseudoverticels of 4, glabrous, petiolate; petioles 14–30 mm by 4–8 mm; lamina chartaceous to subcoriaceous, elliptic to ovate or narrowly ovate, sometimes ± falcate, 150–450(–500) mm by 80–230(–240) mm, the apex acute to acuminate, the base obtusely decurrent to obtusely cuneate or acutely cuneate to acutely decurrent, the secondary veins 7–9 pairs, making a 60–70° angle with the costa, the venation raised and prominent, visible to 4–5° on both surfaces, the margin plane to slightly revolute; seedling and sucker leaves heterophyllous, with 1–3 pairs of serrate teeth in the apical portion, the petiole red when living. Inflorescence basally cauliflorous (exceptionally ramiflorous), on meristematic swellings up to ca. 1 m above ground level, the flowers solitary, fasciculate or in a unisexual or sexually mixed pleiochasium of 3–7, the gynoecious flower often terminal, the floral axis 5–20(–45) mm by 1.2–2 mm, finely pubescent, basally bracteolate. Androecious flower in bud globose, puberulent, 7–8 mm diam., apiculate with 4 minute tepals, the pedicel 25–60 mm by 0.8–1 mm, pubescent, subtended by a minute, caducous deltoid bracteole; at anthesis deeply 4-fid, 14–18 mm diam., the lobes thick, spreading almost flat or slightly incurved, the internal receptacle surface glabrous; stamens numerous, ca. 100–250, obovoid to clavate, 0.8–1.5 mm long by 0.5–0.6 mm wide, the loculi confluent at the obtuse apex (very rarely separate), occupying the apical ½–⅔ of the stamen, the connective not prolonged, the filament distinct, slender. Gynoecious flower in bud napiform-discoid, pubescent, the apex depressed, with an apicule or several pairs of minute tepals, the pubescent pedicel 38–80 mm by 1.5 mm; at anthesis shallowly napiform-discoid, 11–13 wide by 4–6 mm long, the apex splitting into 4(–6) everted deltoid lobes, the orifice ± square or subcircular, comprising ca. ½ total width of the receptacle; styles numerous, ca. 300, shortly conical, 0.6–1 mm long by 0.2–0.3 mm wide basally, the internal receptacle surface velutinous with dense, simple hairs between the styles. Fruiting receptacle solitary at the base of the trunk (exceptionally on the branches), napiform-urceolate or subglobose, 30–56 mm diam. by 22–45 mm long, the orifice ca. 25 mm diam., comprising ca. ½ total width of the receptacle, subentire, bearing remnants of the indurated lobes, the walls ca. 12 mm thick, the external surface corky brown, bumpy, with several prominent veins, the internal surface with numerous shortly conical styles 0.6–1 mm long by 0.2–0.3 mm wide basally, interspersed with scattered simple hairs, the pedicel and peduncle (15–)35–80 mm by 4–5 mm. Mature carpels ovoid-compressed, 12–13 mm long, 6–8 mm wide, 4–5 mm thick, the endocarp light brown, with an irregular network of low ridges, the surface slightly foveate-scrobiculate.

Distribution. Endemic to Mauritius (Fig. 38).

Habitat. Tambourissa amplifolia is local and occasional to common in the lower montane wet forest zone at Bel Ombre (200–400 m), at Plateau Colophane below Macabé Forest (ca. 500 m), on the summit of Mt. Corps de Garde (ca. 750 m), in cloud forest on Mt. Lagrave (500–628 m), and in moist forest on the crest of Piton du Fouge (650 m).

MAURITIUS. BEL OMBRE FOREST: Bel Ombre Nature Reserve, 7 Dec. 1971 (fl), *Guého sub MAU 15195* (K, 2 sheets; MAU); 200–400 m, 27 Dec. 1978 (st), *Lorence 2216* (MO); (st), *Lorence 2217* (MO); (st), *Lorence 2218* (MO); (fl), *Lorence 2219* (MO, Z); (fl), *Lorence 2220* (MO, P); (fl), *Lorence 2221* (K, MO); (fl), *Lorence 2222* (K, MAU, MO, REU); (fl), *Lorence 2223* (MO, P); 10 Jan. 1979 (fl), *Lorence 2259* (MAU, MO); 16 Feb. 1979 (fl), *Lorence 2408* (MO); 3 July 1979 (st), *Lorence 2691* (MO, 2 sheets); (fr), *Lorence 2692* (MO). CORPS DE GARDE MT.: summit ridge, ± stunted forest, 15 Nov. 1973 (fl), *Coode et al. 4066* (K, MAU); 8 Nov. 1971 (fl), *Guého sub MAU 14928* (MAU, 2 sheets). PITON DU FOUGE: crest of Piton du Fouge, low, dryish forest, ca. 600 m, 24 Jan. 1976 (fl), *Lorence 1629* (MAU). MACABÉ FOREST: Plateau Colophane below Macabé, ca. 600 m, 15 Jan. 1979 (st), *Lorence 2280* (MAU, MO); (st), *Lorence 2281* (MO); near Macabé, uplands, ca. 600 m (st), *Vaughan sub MAU 1510* (MAU); Macabé high forest, 660 m, May 1938 (st), *Vaughan sub MAU 1603* (MAU). MT LAGRAVE: 500–600 m, 19 Feb. 1979 (st), *Lorence & Lecordier 2362* (MO). WITHOUT PRECISE LOCALITY: (fl), *Anon. s.n.* (BM); 1863 (fl), *Anon. sub Herb. Blackburn s.n.* (K); (fr), *Anon. sub Herb. Brown s.n.* (K); (fl), *Anon. sub Herb. Cosson s.n.* (P, 2 sheets); 1865 (fl, fr), *Anon. sub Herb. De Candolle 16(2): 659, no. 3* (G, 3 sheets; MO, microfiche); (st), *Anon. sub Herb. Inst. Sci. Madagascar s.n.* (P); (st), *Boivin s.n.* (K, P, possibly isotypes of *T. amplifolia*); 1814 (st), *Carmichael s.n.* (K); ca. 1755 (fr), *Commerson s.n.* (P); (fl), *Commerson 67* (P, 2 sheets); (fl), *s.n. sub Herb. Juss. 16708* (P-JUSS; MO, photo); (st), *Hardwicke s.n.* (G).

Tambourissa amplifolia belongs to species Group 5 and appears to be most closely related to *T. tau,* which differs in having relatively smaller leaves consistently aggregated into pseudoverticels of two to four pairs separated by long "internodes," by its T-shaped stamens with separate loculi, and by its long, setose styles, and internally glabrous gynoecious receptacles. Fruiting carpels of *T. amplifolia, T. pedicellata,* and *T. tau* all have endocarps with a series of low, ± branching ridges, a feature unknown in other species and perhaps suggestive of a close affinity between these species.

Bel Ombre forest harbors the largest known population of *Tambourissa amplifolia,* where it occurs sympatrically with *T. tau.* No intermediates or suspected hybrids were found here despite concurrent flowering times from December to February.

Populations that approach *Tambourissa tau,* however, occur in the eastern mountain ranges of Mt. des Créoles (*Lorence & Julien 2337,* MAU, MO) and also Piton Bambou (*Staub sub MAU 13493,* MAU). Although these plants resemble *T. amplifolia* in having large, acuminate petiolate leaves, their flowers most closely approach *T. tau* in being axillary (in *Staub sub MAU 13493*) and externally corky brown with multiple, incurved orifice lobes and long, setose styles (in *Lorence & Julien 2337*). Stamens are critical in distinguishing the two species; unfortunately, androecious flowers are absent in both collections. Another intermediate collection, without precise locality (*Anon. sub Herb. Brown s.n.,* K), approaches *T. tau* in having ramiflorous, shortly pedicellate fruits, but the shortly conical styles are characteristic of *T. amplifolia*; androecious flowers are absent also.

The holotype of *Tambourissa amplifolia,* either from Grand Port or the Pouce Mt., possesses abnormally short floral pedicels (8–10 mm long) and almost glabrous androecious buds. Although lowland forest in the Grand Port region no longer exists, Boivin's type is similar to recent collections from the nearby Mts. Bambous and Des Créoles in some respects. The type's obovate, obtuse stamens with confluent loculi are characteristic of the species as a whole, as are the broad, petiolate leaves, so there can be no doubt as to which species it represents despite the anomalous pedicels and bud pubescence. As *T. amplifolia* and *T. tau* remain morphologically distinct over much of their range, particularly at Bel Ombre where I studied them, I have decided to regard them as distinct species.

Living flowers of *Tambourissa amplifolia* have externally yellow-green to purple-red receptacles, cream to pale orange-yellow stamens, and pale yellow-pink to dark purple styles. A vague, faintly fruity odor is produced by the flowers.

Vernacular name. Bois tambour (Mauritius).

26. Tambourissa tau Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 303, pl. 3, figs. 14, 15. 1982. TYPE: Mauritius. Perrier Nature Reserve: wet forest with *Sideroxylon* dominant, 600 m, 8 Oct. 1978 (fl), *Lorence 1835* (holotype, MO; isotypes, B, K, MAU, P, Z).

Little-branched monoecious understory treelet, rarely shrubby, 1–4 m tall, the stems to 75 mm diam., the new growth sparsely puberulent or with rare, scattered hairs, the mature leafy stems glabrous, terete, 4–7 mm diam. Leaves opposite, decussate, clustered into pseudoverticels of 2–4 pairs, sessile to subsessile, rarely shortly petiolate, glabrous; petioles stout, 1–8 (–15) mm by 3–6 mm; lamina subcoriaceous to coriaceous, broadly elliptic to narrowly elliptic, obovate or oblanceolate, rarely ovate, (70–)150–300 mm by (30–)45–130 mm, the apex shortly acuminate, shortly acute, obtuse, rounded or retuse, the base subcordate, rounded, obtuse, cuneate or acutely cuneate, the secondary veins (4–)6–9 pairs, making a 50–65° angle with the costa, the venation raised, visible to 3(–4°) adaxially, visible to 4(–5°) abaxially, the margin slightly to moderately revolute; seedling leaves heterophyllous with 2–3 pairs of short, serrate teeth in the apical portion, the petioles red when living. Inflorescence cauliflorous on meristematic swellings along entire length of the stem, occasionally ramiflorous or axillary, the flowers solitary, in a fascicle or dichasium of 2–3, or rarely in a short pleiochasium of 3–6 flowers, sexually mixed or not, the floral axis 2–3(–5) mm by 1–1.5 mm, ± corky, glabrous or sparsely puberulent basally, subtended by several small, ciliate, naviculate-deltoid bracteoles. Androecious flower in bud globose, ± depressed, the apex with several minute, deltoid tepals, the external surface corky brown, mottled, the pedicel 6–20 mm by 1–1.5 mm, basally bracteolate; at anthesis 4–6-fid, 20–25 mm diam., the lobes spreading flat, the internal receptacle surface glabrous; stamens numerous, ca. 100–150, T-shaped, 1–1.5 mm long by 1.5–2 mm wide, the loculi separate on lateral arms (rarely ± sessile, but never confluent), the filament distinct, slender, the connective slightly prolonged apically or not. Gynoecious flower in bud turbinate-depressed to napiform-depressed, 7–10 mm diam. by 4–5 mm long, externally corky brown, apiculate with several minute tepals, the pedicel 6–20(–40) mm by 1–1.5 mm, subtended by several pairs of deltoid bracteoles; at anthesis napiform-urceolate, 10–12 mm diam., the orifice splitting into 5–10 thick, irregularly deltoid, straight or incurved lobes, the orifice 3–6 mm diam., comprising ca. ⅓–½ total width of receptacle; styles numerous, ca. 80–100, slender, setose, 2–3 mm long by 0.3–0.5 mm wide at the ventricose base, the internal receptacle surface glabrous. Fruiting receptacle solitary on the main stem or major branches, rarely axillary or subterminal, shallowly cupuliform-patelliform to subglobose, 25–50 mm diam. by 10–27 mm long, the orifice 10–26 mm diam., comprising ca. ½ total width of the receptacle, subentire with 5–6 indurated deltoid lobes, the walls 10–14 mm thick, the external surface corky brown, bumpy, the internal surface with numerous scattered, setose styles 1.5–3.5 mm long by 0.3–0.4 wide basally, otherwise glabrous, the pedicel stout, 8–20 mm by 2–7 mm. Mature carpels ovoid-compressed, 10–14 mm long, 6–8 mm wide, 4–6 mm thick, with occasional low, irregular ridges, the surface scrobiculate to foveate. Gametic chromosome number, $n = 19$. Figure 39.

Distribution. Endemic to Mauritius (Fig. 38).

Habitat. This is one of the commonest and most widespread members of the genus in Mauritius, occurring in most medium to upper altitude wet and cloud forest communities from ca. 300 to 800 m.

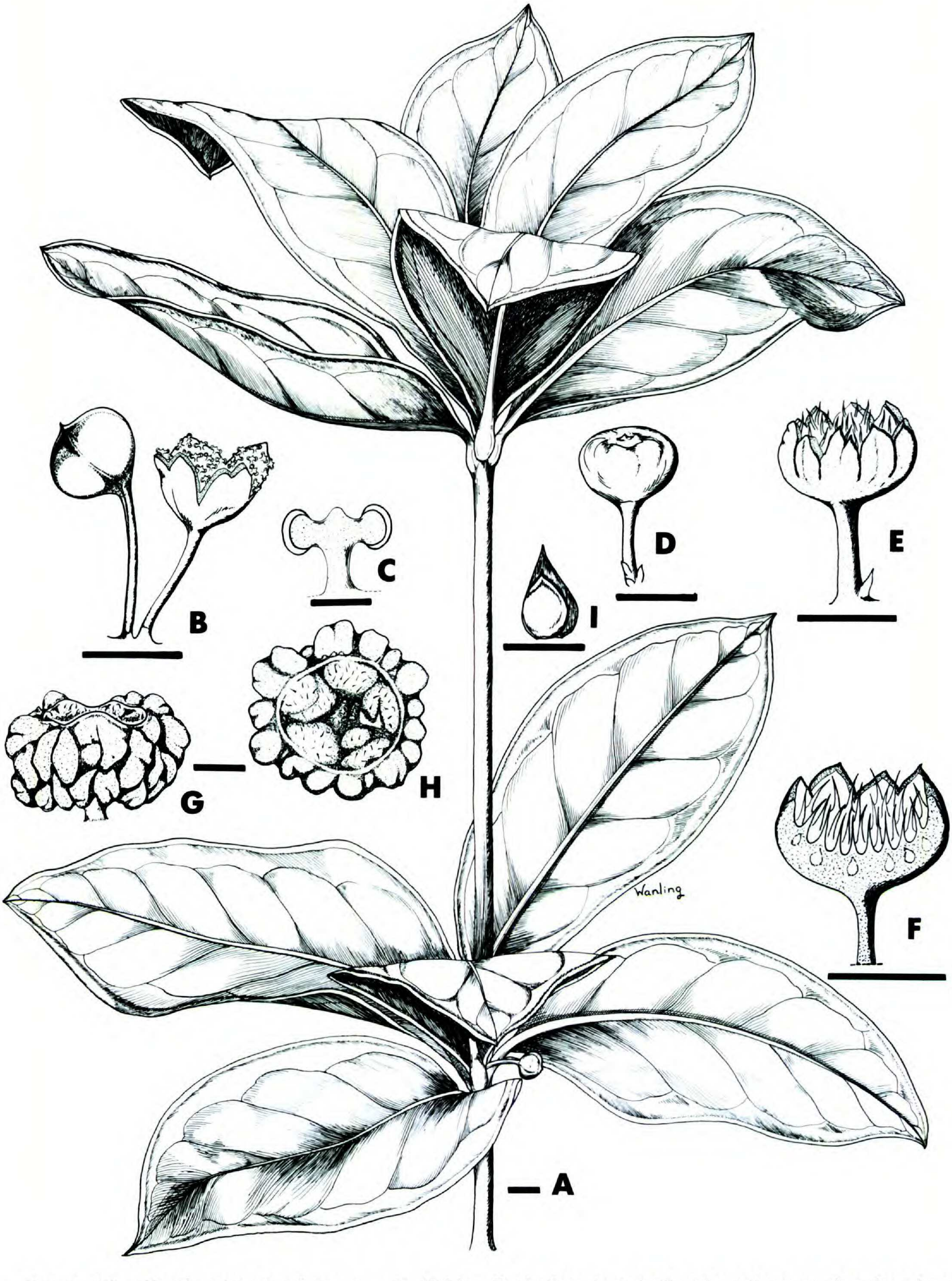

FIGURE 39. *Tambourissa tau* Lorence.—A. Habit.—B. Androecious bud and newly opened androecious flower, lateral view.—C. Stamen, lateral view.—D. Gynoecious flower in bud, lateral view.—E. Gynoecious flower at anthesis, lateral view.—F. Gynoecious flower, longitudinal section.—G. Submature fruiting receptacle, lateral view.—H. As in G, apical view.—I. Fruiting carpel, lateral view. A. Perrier Nature Reserve, Mauritius (Lorence photo, unvouchered). B–F. *Lorence 1835* (MO). G, H. *Lorence 2950* (MO). I. *Lorence 2629* (MO). Bars equal 10 mm in A, B, D–I, and 1 mm in C.

MAURITIUS. BASSIN BLANC: side of track to E side of lake, 550 m, 25 May 1976 (fr), *Richardson et al. 4163* (K). BEL OMBRE FOREST: ca. 200–400 m, 27 Dec. 1978 (fl), *Lorence 2215* (MO); 10 Jan. 1979 (fl), *Lorence 2257* (MO); (fl), *Lorence 2258* (MO). CUREPIPE BOTANICAL GARDEN: near lake, 30 June 1966 (fl), *Vaughan sub MAU 12203* (MAU, 3 sheets). GAULETTES SERRÉES: low mixed wet forest over lava, 400–450 m, 19 May 1979 (fl), *Lorence et al. 2641* (MO). GRAND BASSIN: upland thicket, 22 Sept. 1932 (st), *Orian sub MAU 47* (MAU). MACABÉ FOREST: high forest, 660 m, 18 Oct. 1978 (fl), *Lorence et al. 1863* (MO); Macabé to Brise Fer road, 660 m, 8 Dec. 1978 (fl), *Lorence 2102* (MAU, MO); (fr), *Lorence 2103* (MO); Mare Longue to Macabé road, low indigenous thicket, 1 Nov. 1962 (fl), *Vaughan sub MAU 10472* (MAU). MIDLANDS: vestige of indigenous vegetation along river, 400 m, 9 Feb. 1979 (fl), *Lorence & Lecordier 2357* (MO). MONTAGNE COCOTTE: cloud forest, 770 m, 1 Dec. 1978 (st), *Lorence 1975* (MO); (fl), *Lorence 1976* (MAU, MO); (fl), *Lorence 1977* (MAU, MO); 19 Dec. 1978 (fl), *Lorence & Lecordier 2161* (MAU, MO); (st), *Lorence & Lecordier 2165* (MO). MONTAGNE DES CRÉOLES: transitional evergreen forest, 250–300 m, 25 Jan. 1979 (fl), *Lorence & Julien 2337* (MAU, MO); (st), *Lorence & Julien s.n.* (MAU). MONTAGNE LAGRAVE: flank facing Eau Bleue reservoir, 5 Apr. 1974 (fr), *Coode et al. sub MAU 17615* (MAU); N part, summit area, degraded cloud forest invaded by exotics, 500–600 m, 9 Feb. 1979 (fl), *Lorence & Lecordier 2363* (MO); S slope facing Eau Bleue reservoir, cloud forest invaded by exotics, 600 m, 24 May 1979 (fr), *Lorence & Lecordier 2649* (MO). PERRIER NATURE RESERVE: dense indigenous thicket, 14 May 1970 (fr), *Guého sub MAU 14297* (MAU); lower montane wet forest, ca. 600 m, 8 Oct. 1978 (fl), *Lorence 1836* (MO); (fl), *Lorence 1837* (MO); 13 Oct. 1978 (st), *Lorence 1841* (MO); 12 May 1979 (fr), *Lorence 2628* (K, MAU, MO, P); (fr), *Lorence 2629* (MO); Perrier near Mare aux Vacoas, 10 Sept. 1937 (st), *Vaughan sub MAU 1404* (MAU); 25 Oct. 1962 (fl), *Vaughan sub MAU 10473* (MAU). PÉTRIN NATURE RESERVE: low *Sideroxylon* wet forest, 630 m, 12 Dec. 1978 (fl), *Lorence 2122* (MAU, MO). PITON BAMBOU: near crest of hill on the leeward side, 14 Aug. 1968 (fl), *Staub sub MAU 13493* (MAU; approaches *T. amplifolia*). PITON DE LA RIVIÈRE NOIRE: lower montane wet forest, 700–827 m, 25 Nov. 1978 (fl), *Lorence 1964* (MAU, MO); 26 Dec. 1978 (fl), *Lorence 2204* (MO). PLAINE LIEVRE: by side of road to Brise Fer, indigenous thicket, 9 Mar. 1969 (fr), *Guého sub MAU 13750* (MAU); stunted forest around clearing, 600 m, 27 Aug. 1979 (fl), *Lorence et al. 2923* (K, MO). VALLEY OF CASCADE 500 PIEDS: *Calophyllum*/Sapotaceae wet forest, 550 m, 18 May 1979 (fl), *Lorence 2634* (MO). WITHOUT PRECISE LOCALITY: (fr), *Anon. sub Herb. Richard s.n.* (P); 14 Jan. 1930 (fl, fr), *Vaughan 382* (K, 3 sheets).

Tambourissa tau is most closely allied to *T. amplifolia,* with which it has been confused in the past (e.g., Vaughan & Wiehe, 1937, 1941, in their vegetational sampling analyses at Mt. Cocotte, Macabé Forest and Perrier). Both belong to species Group 5 and have large leaves, making them difficult to separate vegetatively, although they are easily separable by floral characters. *Tambourissa amplifolia* has pubescent inflorescences, internally velutinous gynoecious flowers with shorter, non setose styles, and apically confluent anther loculi never found in *T. tau* (see *T. amplifolia* for further discussion). The specific epithet *tau* is Greek, Latin, and Celtic for "T," referring to the characteristically T-shaped stamens which are unique in the entire genus.

A plant growing in the Curepipe Botanical Garden (*Vaughan sub MAU 12203,* MAU) is typical of *Tambourissa tau* in all characters except the anomalous staminal loculi, which are sessile and not borne on extended lateral arms, although neither are they apically confluent as in *T. amplifolia.* Furthermore, gynoecious flowers of *Vaughan sub MAU 12203* are typical of *T. tau.* Flynn and Rowley (1972) studied the ultrastructural development of the pollen wall of this same plant as *T. amplifolia.*

Flower color morphs with either dark reddish purple or pale pink to greenish white stamens and styles occur; these are generally constant within a given population (e.g., dark red-purple as Perrier, pale pink or white at Mt. Cocotte). The flowers produce no apparent odor.

Vernacular name. Bois tambour (Mauritius).

27. **Tambourissa tetragona** (Boiv. ex Tul.) A.DC., Prodr. 16(2): 659. 1868; Baker, Fl. Mauritius 289. 1877; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901. *Ambora tetragona* Boiv. ex Tul., Ann. Sci. Nat. (Paris) 4(3): 30. 1855; Tul., Monogr. Monim. 302. 1855. TYPE: Ile de France (Mauritius). Without precise locality (ca. 1755) (st), *Commerson s.n.* (lectotype, P, here designated).

Dioecious (?), sparsely branching slender treelet or small tree attaining 6 m tall and 10 cm D.B.H., the bark pale brown, smooth with longitudinal fissures, the new growth glabrous, the mature leafy stems quadrangular, 4–6 mm diam., with 4 low wings ca. 1–1.5 mm wide. Leaves opposite, rarely subopposite, petiolate, glabrous; petioles stout, 5–15 mm by 2–3 mm, winged, the wings decurrent onto the stem; lamina subcoriaceous, narrowly obovate, oblanceolate, narrowly oblong or rarely narrowly elliptic, 52–180 mm by 17–48 mm, the apex shortly acuminate, rarely shortly acute, the tip indurated, the base acute, strongly decurrent along the petiole, the

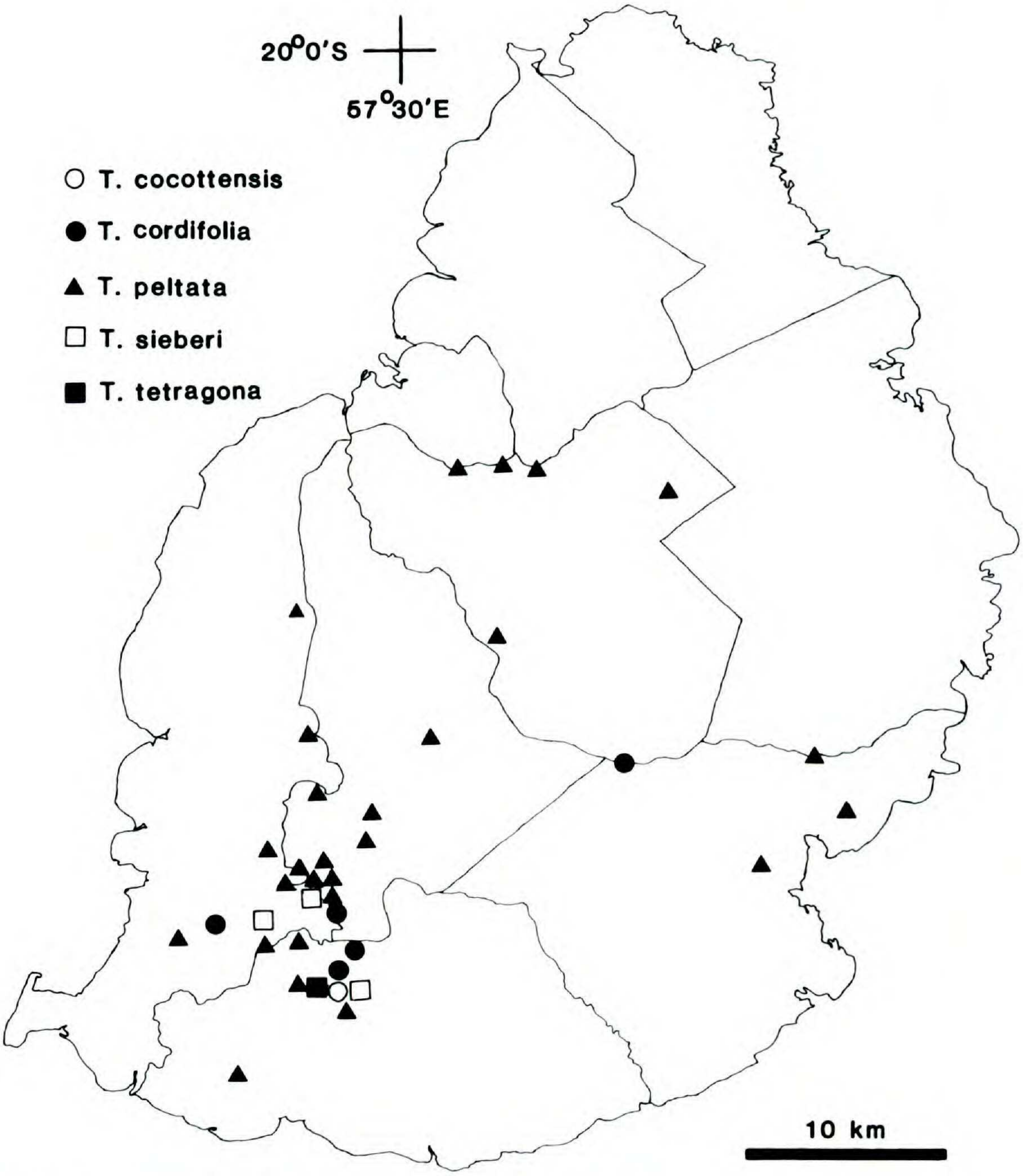

FIGURE 40. Distribution map of some *Tambourissa* species in Mauritius.

secondary veins 8–13 pairs, making a 65–80° angle with the costa, the venation obscure, visible to 2° on both surfaces, the margin revolute. Cauliflorous, the androecious inflorescence (fide Tulasne) a sparse pleiochasium, the buds globose, inaperturate, shortly pedicellate, the stamens and mature androecious flowers unknown; gynoecious inflorescence a short, glabrous, rarely leafy pleiochasium of 5–11 flowers, the floral axis quadrangular, 7–13 mm by 2–2.5 mm, subtended by several pairs of glabrous, decussate naviculate bracteoles 1 mm by 0.5 mm, the pedicel 3–4 mm by 1.5–2 mm, subtended by a glabrous, deltoid bracteole 1–2.5 mm long. Gynoecious flower in bud napiform-depressed, 8–10 mm diam. by 6–8 mm long, apiculate with 4 small, glabrous obtuse tepals, the external surface drying wrinkled, glabrous, the walls thick; at anthesis the apex splitting into 4(–5) deltoid lobes ca. 3 mm long and wide, the orifice small, ca. 1 mm wide, X-shaped, the lobes hirsute internally; styles numerous, ca. 200, shortly conical, 0.6–0.8 mm long by 0.5–0.7 mm wide at the strongly ventricose base, the internal receptacle surface glabrous between the styles. Fruiting receptacle and carpels unknown.

Distribution. Endemic to Mauritius (Fig. 40).

Habitat. *Tambourissa tetragona* is presently known only from low cloud forest on the summit of Mt. Cocotte at the southern extremity of the central plateau.

MAURITIUS. GRAND PORT: woods of the Grand Port District, Aug. 1851 (st), *Boivin s.n.* (P, syntype). MONTAGNE COCOTTE: Aug. 1977 (st), *Friedmann 3201* (P); summit, 11 Dec. 1979 (st), *Guého & Lecordier sub MAU 19501* (MAU); low, degraded cloud forest on summit, 770 m, 19 Dec. 1978 (st), *Lorence & Lecordier 2164* (MO); (st), *Lorence & Lecordier 2166* (K, MAU, MO); 17 Jan. 1979 (st), *Lorence 2286* (MO); 30 Aug. 1979 (fl), *Lorence et al. 2928* (MO); Dec. 1937 (fl), *Vaughan sub MAU 1508* (MAU); (fl), *Vaughan sub MAU 1706* (MAU). WITHOUT PRECISE LOCALITY: (st), *Anon. sub Herb. Richard s.n.* (P).

The leaves, female receptacle, and styles of *Tambourissa tetragona* are morphologically similar to those of *T. cocottensis,* a species also confined to a small patch of cloud forest on the summit of Mt. Cocotte, one of the island's highest and wettest spots. Although androecious flowers and fruiting receptacles of the former are required to further assess its affinity, both belong to species Group 5. The distinctive quadrangular, winged stems of *T. tetragona,* however, set it apart from all other members of the genus.

In the living state, leaves of *Tambourissa tetragona* have a lustrous, dark green lamina and red petiole, the stems being pale green with transluscent wings. Vegetatively, it is one of the most attractive members of the genus. Gynoecious buds are shiny green flushed with dark red-purple. Buds are initiated in July and August and appear to mature in December. Known only from a single, small population in a highly degraded habitat, the species should be considered endangered. My attempts to propagate it vegetatively by cuttings failed.

Vernacular name. Bois tambour (Mauritius).

28. **Tambourissa cocottensis** Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 295, pl. 1, fig. 2. 1982. TYPE: Mauritius. Low cloud forest, summit of Mt. Cocotte, 760 m, 19 Dec. 1978 (fl, fr), *Lorence & Lecordier 2167* (holotype, MO; isotype, MAU).

Monoecious treelet or small tree 4–5 m tall and 10–35 cm D.B.H., often multistemmed from coppices, the new growth glabrous, the mature leafy stems terete, 2–4 mm diam., longitudinally striate. Leaves opposite to subopposte, petiolate, glabrous; petioles 7–20 mm by 1–2 mm; lamina subcoriaceous, elliptic, 45–105 mm by 15–40 mm, the apex shortly acute to shortly acuminate, the tip indurated, the base acutely cuneate, slightly decurrent, the secondary veins 6–9 pairs, making a 55–65° angle with the costa, the venation visible to 3° on both surfaces, slightly raised, the margin moderately revolute. Androecious flowers solitary or in fascicles of 2, borne along the trunk. Androecious flower in bud globose, apiculate, 6 mm diam., externally corky brown, the pedicel and peduncle 4–5 mm by 1.5 mm, quadrangular, pilose, bearing 4 decussate rows of bracteoles 1 mm long; at anthesis 4–7-fid, the lobes spreading flat, 20–21 mm diam., reddish pink; stamens ca. 150–200, subsessile, linear-subulate, 3 mm by 0.6–0.8 mm, the loculi lateral, free, occupying ca. ⅔–¾ total length of stamen, the connective prolonged, slender, 1 mm long, the internal receptacle surface glabrous. Gynoecious inflorescence cauliflorous from meristematic swellings along the basal 1 m of the trunk, the flowers solitary or in fascicles of 2. Gynoecious flower in bud napiform-depressed, 9–11 mm diam. by 5–7 mm long, the apex bearing 3–4 minute, pubescent deltoid tepals, the external receptacle surface pale corky brown with scattered simple hairs, the pedicel and peduncle 4–7 mm by 1–1.5 mm, jointed near the base, quadrangular, pilose, bearing 4 decussate rows of minute, ciliate naviculate bracteoles 1–1.5 mm long; at anthesis the apex splitting into 5–7 irregular, ± inflexed deltoid lobes, the orifice comprising ca. ⅓ total width of the receptacle; styles numerous, ca. 150–200, narrowly conical, setose, 1.5–2 mm long by 0.2–0.3 mm diam. at the slightly ventricose base, the apex long acuminate, the internal receptacle surface with scattered clusters of simple hairs between the styles. Young, submature fruiting receptacle globose-urceolate, 15 mm diam. by 12 mm long, the apex depressed, the orifice subcircular, 3–4 mm diam., with 5–7 thick, deltoid lobes, comprising ca. ¼–⅕ total width of the receptacle, the external surface mottled corky brown, the internal surface with numerous setose styles 1.5–2 mm long by 0.5 mm wide basally, pilose between the styles and on the lobes, the peduncle and pedicel 5 mm by 3 mm. Mature fruiting receptacle and carpels unknown. Figure 41.

Distribution. Endemic to Mauritius (Fig. 40).

Habitat. *Tambourissa cocottensis* is known only from a single population on the summit of Mt. Cocotte in low cloud forest (annual precipitation 5,000 mm). Extensive searching revealed only four individuals growing within an area ca. 100 m across.

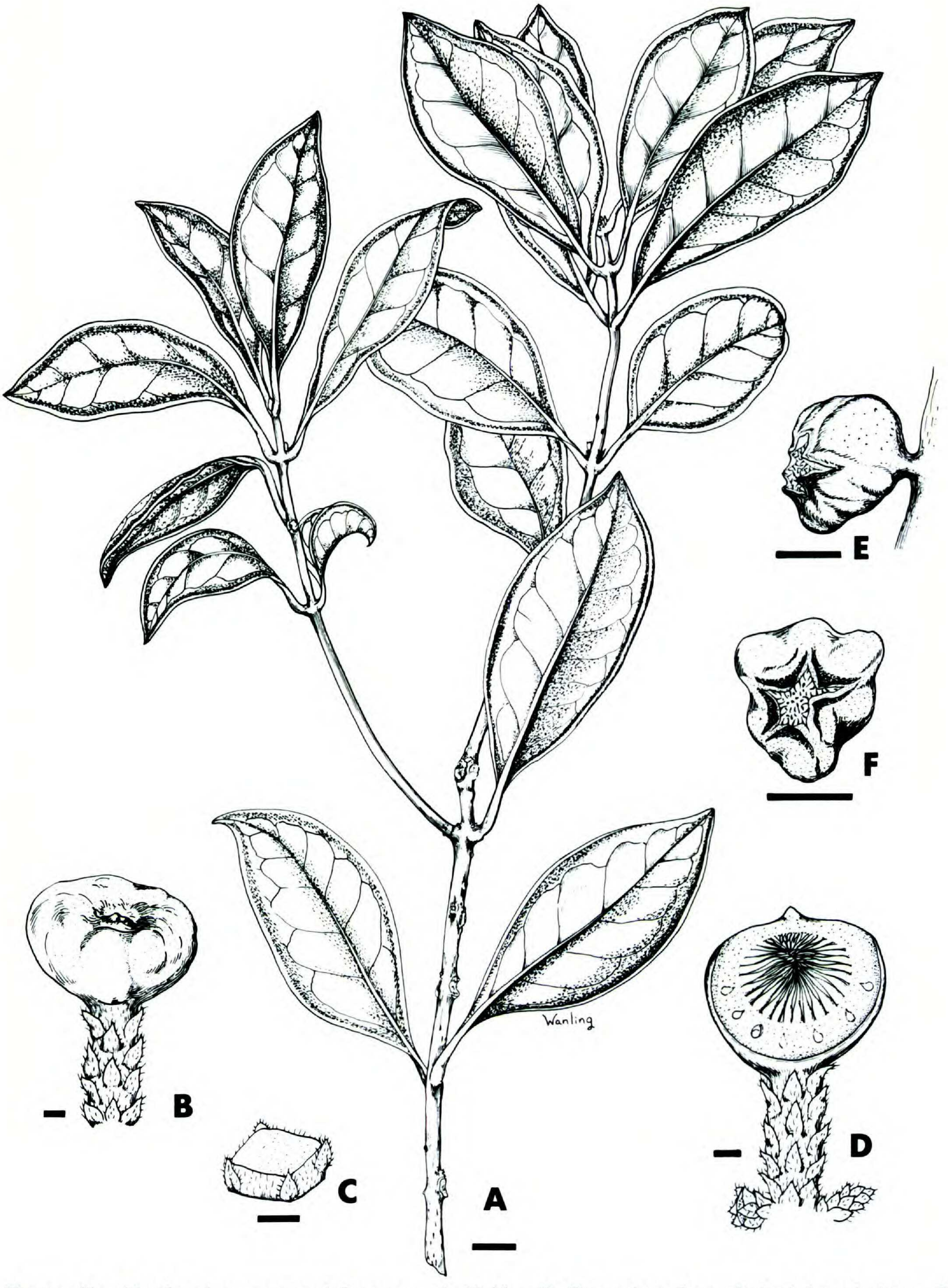

FIGURE 41. *Tambourissa cocottensis* Lorence.—A. Habit.—B. Gynoecious flower in bud, lateral view.—C. Gynoecious floral pedicel, transverse section.—D. Gynoecious flower in bud, longitudinal section.—E. Submature fruiting receptacle, lateral view.—F. As for E, apical view. A. *Lorence 2288* (MO). B–D. *Lorence 2287* (MO). E, F. *Lorence 2167* (MO). Bars equal 10 mm in A, E, F, and 1 mm in B–D.

MAURITIUS. MONTAGNE COCOTTE: summit region, low degraded cloud forest, 760 m, 17 Jan. 1979 (fr), *Lorence 2287* (K, MO, P); (st), *Lorence 2288* (MO); crest, 14 July 1982 (fl), *Lecordier sub MAU 20412* (MAU); 23 Sept. 1983 (fl), *Lecordier & Strahm sub MAU 20563* (MAU).

Tambourissa cocottensis closely resembles *T. tetragona* in a number of respects, including leaf size, shape, texture, margin, and venation, but lacks the winged stems and petioles of the latter. Both are cauliflorous with structurally similar flowers, but those of *T. cocottensis* are solitary or in fascicles of two and externally corky, differing from the smooth, glabrous pleiochasial flowers of *T. tetragona.* They more closely resemble those of *T. tau,* except for the distinctive quadrangular floral pedicels bearing four decussate rows of ciliate bracteoles. Both *T. cocottensis* and *T. tetragona* belong to species Group 5, although the prolonged staminal connectives of the latter are suggestive of certain Madagascan species.

The four known individuals of *Tambourissa cocottensis* are of different size classes, suggesting some regeneration has taken place in recent years. The two largest individuals (both gynoecious) were in bud in August 1979, and young fruits were present in December 1978 and January 1979; androecious flowers were not found. Although officially a nature reserve, the forest on Mt. Cocotte is highly degraded and has undergone extensive invasion by vigorous, weedy exotic plant species. As a result, there is a grave danger that the population is too small to maintain itself, as is also the case for *T. tetragona.* Both appear to be relictual species confined to the summit of Mt. Cocotte.

29. **Tambourissa cordifolia** Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 296, pl. 1, figs. 5, 6. 1982. TYPE: Mauritius. Pétrin Nature Reserve: low *Philippia* heath formation, 630 m, 15 May 1979 (fl, fr), *Lorence 2631* (holotype, MO; isotype, K).

Glabrous dioecious shrub, rarely a small treelet, the multiple erect stems 50–200 cm tall and 6–10 mm diam., the mature leafy stems 2–4 mm diam., longitudinally striate. Leaves opposite, decussate, subsessile or sessile, glabrous; petiole 1–1.5 mm long by 2–3 mm wide; lamina subcoriaceous, ovate to elliptic, 30–80 by 25–55 mm, the apex shortly acute, obtuse or retuse, often rounded or mucronulate, the base cordate, rarely subtruncate, the secondary veins 5–6 pairs, making a 50–60° angle with the costa, the venation raised and visible to 3(–4°) adaxially and to 4(–5°) abaxially, the margin slightly revolute; seedling leaves heterophyllous, the petioles short, red when living, the lamina narrowly elliptic, entire or with 1–2 pairs of small teeth apically. Inflorescence glabrous, either ramiflorous on leafless nodes or cauliflorous, the flowers solitary or in fascicles of 2(–3), very rarely in a short di- or pleiochasium of 3(–5) flowers, or the flowers rarely solitary and axillary or terminal on leafy shoots. Androecious flower in bud globose, 10–16 mm diam., the apex with 4 minute, obtusely deltoid tepals, the pedicel and peduncle jointed basally, 9–30(–50) mm by 1–1.5 mm, bearing basally 1–3 pairs of apically ciliate, deltoid bracteoles; at anthesis 4(–5)-fid, 28–36 mm diam., the lobes spreading flat, then reflexing; stamens numerous, ca. 300–400, narrowly ellipsoid or clavate, 1–2 mm by 0.5–1 mm, the loculi occupying ½–¾ total length of the stamen, usually separate, sometimes confluent basally into a U-shape, or confluent apically at the obcordate apex, the connective not prolonged, the internal receptacle surface bearing scattered hairs. Gynoecious flower in bud napiform-depressed, apiculate with 4 minute tepals, the pedicel and peduncle jointed basally, 10–15 mm by 1–1.5 mm, basally bracteolate as in male flower; at anthesis shallowly napiform-urceolate, 8–12 mm diam. by 4–6 mm long, the orifice splitting into 4(–6) outcurved deltoid lobes, 5–8 mm diam., comprising ½–⅔ total width of the receptacle, the internal surface of the lobes shallowly rugose, glabrous; styles numerous, ca. 100–400, shortly conical, 0.8–1 mm long by 0.4–0.5 mm wide basally, the apex papillose, the internal receptacle surface with clusters of simple hairs between the styles. Fruiting receptacle solitary on the stems, patelliform to shallowly cupuliform, 25–60 mm diam. by 13–40 mm long, the orifice 16–40 mm diam., comprising ½–¾ total width of the receptacle, the rim subentire with 4–6 indurated deltoid lobes, the walls 8–12 mm thick, the external surface corky brown, the internal surface with numerous short, conical styles 0.5–1 mm long by 0.5 mm wide basally, interspersed with clusters of hairs, the pedicel and peduncle 16–25 mm by 2–3 mm. Mature carpels 12–13 mm long, 6–8 mm wide, 5–6 mm thick, ovoid-compressed, the endocarp dark brown, the surface scrobiculate. Gametic chromosome number, $n = 19$. Figure 42.

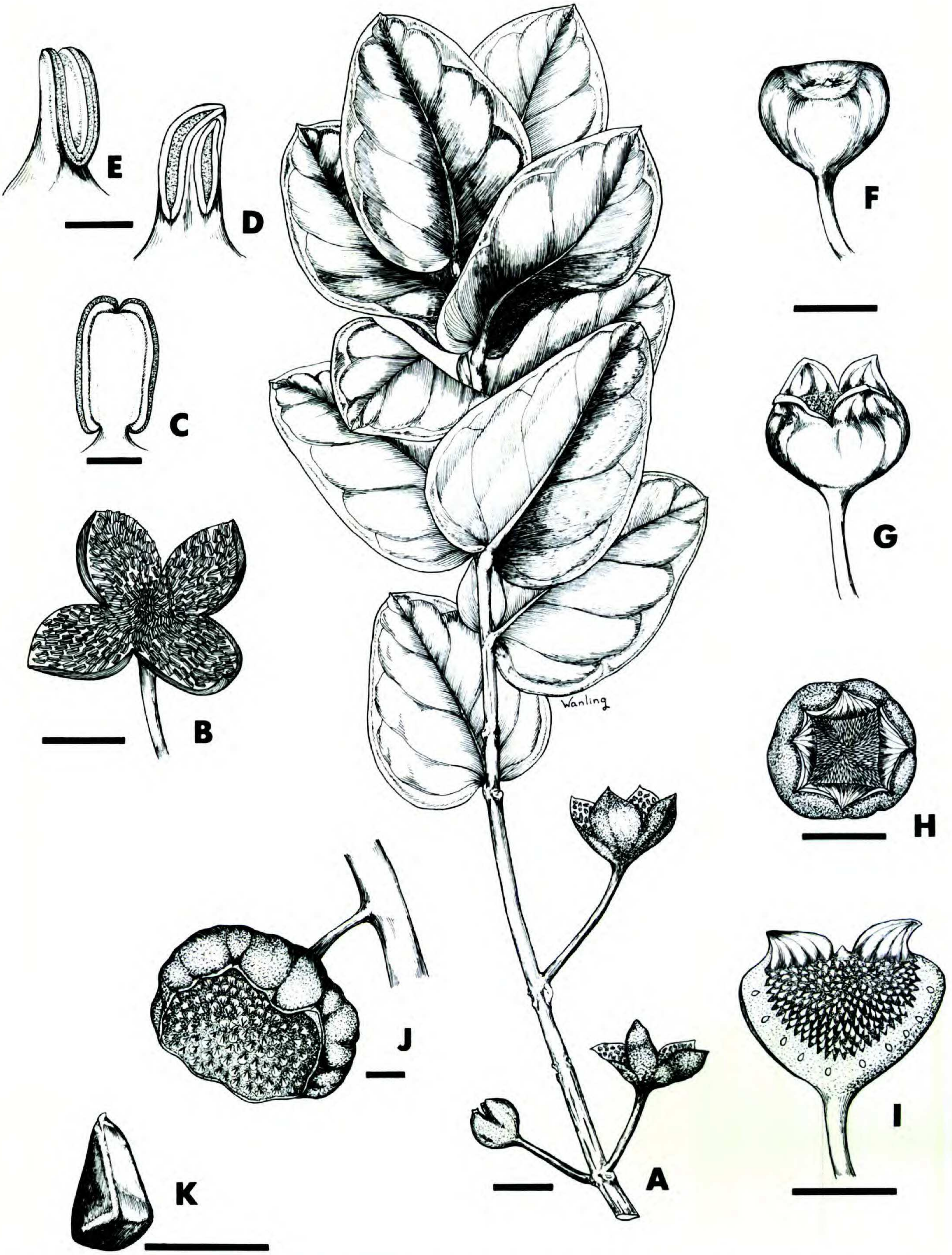

FIGURE 42. *Tambourissa cordifolia* Lorence.—A. Habit, male.—B. Androecious flower at anthesis, apical view.—C. Stamen with free loculi, abaxial view.—D. Stamen with free loculi, adaxial view.—E. Stamen with basally confluent loculi, adaxial view.—F. Gynoecious flower in bud, lateral view.—G. Gynoecious flower at anthesis, lateral view.—H. Gynoecious flower at anthesis, apical view.—I. Gynoecious flower at anthesis, longitudinal section.—J. Submature fruiting receptacle.—K. Fruiting carpel, lateral view. A–E. *Lorence 2632* (MO). F–I. *Lorence 2630* (MO). J, K. *Lorence 2631* (MO). Bars equal 10 mm in A, B, F–K, and 1 mm in C–E.

Distribution. Endemic to Mauritius (Fig. 40).

Habitat. *Tambourissa cordifolia* is restricted to upland regions of hard, unweathered ground water laterite or "cuirasse" supporting low scrub formations, often of *Philippia* heath. It is particularly abundant at Pétrin (630 m, annual precipitation 4,000 mm), and also occurs in comparable *Philippia* heath on Mt. Laselle (550 m, annual precipitation 4,500 mm), in low, marshy scrub at Les Mares near the base of Mt. Cocotte (650 m, annual precipitation 4,800 mm), at Crown Land Declerc, and in low thicket near the summit of Piton de la Rivière Noire (827 m, annual precipitation 4,200 mm).

MAURITIUS. CROWN LAND DECLERC: 15 Aug. 1968 (fl), *Vaughan sub MAU 13343* (MAU). LES MARES: track from Plaine Paule to Mt. Cocotte, 650 m, 13 May 1979 (fl), *Lorence 2626* (MO); 10 Aug. 1979 (fl), *Lorence 2894* (MO). MARE LONGUE PLATEAU: June 1977 (fl), *Friedmann 3132* (P). MONTAGNE LASELLE: N flank, 4 Oct. 1973 (fl), *Lorence sub MAU 16282* (MAU); Midlands, exposed situations, Mar. 1931 (fr), *Vaughan sub MAU 729* (MAU). PÉTRIN NATURE RESERVE: low indigenous thicket, 2 June 1971 (fr), *Guého sub MAU 14762* (MAU); *Phylica/Philippia* heath on lateritic soil, Oct. 1975 (fl), *Guého sub MAU 17585* (MAU, 2 sheets); indigenous thicket near Pétrin, 2,150 ft. (630 m), 23 Mar. 1963 (fr), *Lalouette sub MAU 10337* (MAU); low *Philippia* heath formation, 630 m, 23 Apr. 1973 (fl), *Lorence M 113* (K, MO); (fl, fr), *Lorence M 114* (K, 2 sheets; MO); 26 May 1973 (fl), *Lorence M 144* (K, MO); 12 Dec. 1978 (fr), *Lorence 2119* (MAU, MO); 10 Feb. 1979 (fr), *Lorence 2378* (MAU, MO, P); 4 Apr. 1979 (fl), *Lorence 2571* (MO); 15 Apr. 1979 (fr), *Lorence 2595* (MAU, MO); 9 May 1979 (fl), *Lorence 2618* (MO); 12 May 1979 (fl), *Lorence 2623* (MO); 15 May 1979 (fr), *Lorence 2630* (MO); (fl), *Lorence 2632* (MAU, MO); 22 May 1979 (fl), *Lorence 2645* (MO, P, Z); (fr), *Lorence 2646* (MO); 19 June 1979 (st), *Lorence 2660* (MO); 1 May 1976 (fl), *Richardson et al. 4074* (K); (fl), *Richardson et al. 4075* (K); (fr), *Richardson et al. 4076* (K); (fr), *Richardson et al. 4077* (K); Crown Land Pétrin, 17 June 1939 (fl), *Vaughan sub MAU s.n.* (MAU); (fr), *Vaughan 729* (MAU); Aug. 1937 (fl), *Vaughan sub MAU 1400* (MAU, 2 sheets); 6 June 1969 (fl, fr), *Vaughan sub MAU 13776* (MAU). PITON DE LA RIVIÈRE NOIRE: (fl), *Randabel sub MAU 679* (MAU). WITHOUT PRECISE LOCALITY: (st), right hand leafy collection only, *Anon. sub MAU 1314* (MAU).

Its sessile, cordate leaves and shrubby habit are presumably adaptations to the unique ecological niche which *Tambourissa cordifolia* occupies. Among other Mascarene species of the genus, it appears to be most closely allied to *T. amplifolia* in terms of floral morphology. Both are cauliflorous (rarely ramiflorous) species with long pedicellate, often solitary flowers, the androecious flowers being 4-fid, internally white, and having numerous clavate stamens, the gynoecious receptacles being napiform, opening by 4(–6) everted deltoid lobes, and having numerous short, conical styles interspersed with hairs. *Tambourissa amplifolia* is readily distinguishable by its larger habit, basal cauliflory, monoecy, pubescent inflorescences with longer pedicels and smaller floral receptacles, and very much larger, non-cordate petiolate leaves. Both belong to species Group 5.

The only other dioecious Mauritian species besides *Tambourissa cordifolia* is *T. peltata,* which has ternate to subalternate leaves and belongs to species Group 9. Although the two species are known to hybridize naturally, at least one such hybrid (*Lorence 2624,* MO) is highly sterile with ca. 95% aborted pollen grains.

In living material, the flower buds and outer surface of the receptacle are cream or yellowish flushed with purple-red. The inner, staminal surface of the androecious flowers and lobes of the gynoecious flowers are creamy white and the styles purple-red. Flowers of both sexes produce strong, fruity odors akin to that of ripe apricots or stewed ripe bananas.

Vernacular name. Bois tambour (Mauritius).

30. Tambourissa sieberi (Tul.) A.DC., Prodr. 16(2): 660. 1868; Baker, Fl. Mauritius 287. 1877; Perk. & Gilg, Pflanzenr. 4, 101: 68. 1901; Vaughan, Mauritius Inst. Bull. 1(1): 76. 1937. *Ambora sieberi* Tul., Ann. Sci. Nat. (Paris) 4(3): 31. 1855; Tul., Monogr. Monim. 304. 1855. TYPE: Mauritius. Without precise locality (ca. 1822) (fl), *Sieber Fl. Maurit. II, 316* (holotype, P; isotypes, G, K).

A. vestita Tul., Ann. Sci. Nat. (Paris) 4(3): 31. 1855; Tul., Monogr. Monim. 306. 1855. *Tambourissa vestita* (Tul.) A.DC., Prodr. 16(2): 660. 1868; Cordem., Fl. Réunion 301. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 69. 1901. TYPE: "Bourbon?" (probably Mauritius), without precise locality (ca. 1755), *Commerson s.n.* (holotype, P).

Monoecious tree 10–15 m tall and 30–40 cm D.B.H., the bark light brown, flaking, the new growth velutinous-tomentose with simple, yellowish wavy hairs, the mature leafy stems velutinous, terete, 2–5 mm diam. Leaves opposite to subopposite, petiolate; petioles velutinous, 5–15 mm by 1–1.5 mm; lamina chartaceous to subcoriaceous, both surfaces tomentose-pubescent when young, adaxially glabrescent, elliptic to broadly elliptic, rarely obovate or suborbiculate, 40–76 mm by 18–40 mm, the apex shortly acuminate, acute, rarely obtuse, the base acutely cuneate to acute, the secondary veins 4–7 pairs, making a 60–70° angle with the costa, the venation visible to 2(–3°) adaxially, and to 3(–4°) abaxially, the margin revolute. Inflorescence cauliflorous on mid to upper part of the trunk and on the major branches, an erect, generally unisexual, rarely leafy thyrse of 16–90 flowers, irregularly branching to 2(–3°), all parts pale yellowish velutinous-tomentose, the floral axis stout, 50–310 mm by 3–8 mm, flattened and dialated at the nodes, the secondary axes opposite to subopposite, ± ascendant, 6–90 mm by 2–4 mm, the ultimate branches bearing cymose units of 1–4 flowers, the buds of both sexes globose, 12–14 mm diam., velutinous, apiculate, the apex crowned with 2–3 pairs of persistent, decussate velutinous naviculate tepals 1.5–2.5 mm long by 1 mm wide, the pedicels and peduncles often subtended by a subulate, velutinous caducous bracteole 2–3 mm long, or rarely by a leaf, the pedicels 10–25 mm by 1.5–2 mm. Androecious flower at anthesis deeply (4–)5(–6)-fid, 25–35 mm diam., the lobes spreading flat; stamens numerous, ca. 100–140, ovoid to ellipsoid or oblong, 2–5 mm long by 1–2 mm wide, subsessile, the loculi lateral, separate, occupying almost the entire length of the stamen, the filament broad, short or sessile, the connective broad, slightly prolonged or not, the apex obtuse to emarginate, the internal receptacle surface glabrous. Gynoecious flower at anthesis globose, 15–18 mm diam., the orifice subcircular, 2–4 mm diam., with 4–6 irregular, shallow lobes; styles numerous, ca. 850–875, narrowly conical to setose, 3–4 mm long by 0.4–0.5 mm wide basally, coalescent into groups of 12–30, the internal receptacle surface densely velutinous between the styles. Fruiting receptacles produced on the trunk and major branches, in clusters of 3–15, the major axis 15–20 mm diam., woody, the secondary axis ca. 12 mm diam., the pedicel and peduncle 10–35 mm long by 6–15 mm diam., the receptacle irregularly globose-urceolate, depressed, 55–160 mm diam. by 35–75 mm long, the orifice small, comprising ca. ¼–⅓ total width of the receptacle, the walls 18–20 mm thick, externally pale corky brown, internally with numerous setose styles 2.5–3.5 mm long by 0.5–0.6 mm wide basally, the sides channelled, the surface sparsely tomentose between the styles. Mature carpels ovoid-compressed, 10–13 mm long, 6–7 mm wide, 4–5 mm thick, the smooth endocarp pale brown. Gametic chromosome number, $n = 19$.

Distribution. Endemic to Mauritius (Fig. 40).

Habitat. Isolated individuals and small populations of *Tambourissa sieberi* are known from mature wet forest at Macabé (660 m) and in the Black River Gorges (400–500 m) where the annual precipitation is ca. 3,200–3,400 mm, and also from low cloud forest on Mt. Cocotte (650–760 m, annual precipitation ca. 5,000 mm). Although the species appears to set fruit readily and several seedlings presumably of *T. sieberi* were found at Mt. Cocotte, no recent regeneration was observed at any of the other sites, undoubtedly due to severe competitional pressures exserted by vigorously invasive exotic species.

Although Tulasne thought that the sterile type of *Ambora vestita* may have been collected in Réunion (formerly Bourbon) by Commerson, he in fact questioned the origin of the specimen. Commerson actually did collect in Réunion (Ly-Tio-Fane, 1976), but a number of his other collections are wrongly labelled. I therefore suspect that the type of *Tambourissa vestita* is actually from Mauritius where he collected more extensively. That the type of *T. sieberi* lacks leaves also seems to have prompted Tulasne to describe the Commerson specimen as a new species. In any case, no tomentose *Tambourissa* has ever been subsequently collected or noted from Réunion (Cordemoy, 1895; Rivals, in herb.; Cadet, pers. comm.). Because the type of *T. vestita* is indistinguishable from material of *T. sieberi,* I consider the species synonymous and have chosen to retain the latter name because the type has flowers and is more widely distributed in herbaria.

MAURITIUS. BLACK RIVER GORGES: 1 Dec. 1933 (fl), *Carcenac sub MAU 794* (MAU); Crown Land Le Bouton in Black River Gorges, primary wet forest, ca. 400 m, 10 Jan. 1976 (fl), *Lorence 1585* (K, 2 sheets; MAU, 2 sheets; MO). MACABÉ FOREST: (fl) (prob. Dec. 1973), *Bernardi sub MAU 12873* (G, MAU); Plateau Macabé, 12 Mar. 1933 (fl), *Carcenac 48 sub MAU 1313* (MAU); Crown Land Macabé, 20 Jan. 1950 (fr), *Dulgeet sub MAU s.n.* (MAU); left hand side of path to Macabé plot, 20 Dec. 1965 (fr), *Forest Department sub MAU 11935* (*carpol. coll. 161*) (MAU); upland forest of Macabé (fr), *Forestry Dept. sub MAU s.n.* (MAU); in plot, 6 Jan. 1967 (fl), *Vaughan sub MAU 12498* (MAU); just outside of plot, 6 Jan. 1967 (fl), *Vaughan sub MAU 12499* (MAU, 2 sheets); in plot, 18 Jan. 1976 (fr), *Vaughan sub MAU 13092* (MAU, 2 sheets); 16 Feb. 1967 (fl), *Vaughan sub MAU 13094* (MAU); corner of plot near road, 11 July 1968 (fr), *Vaughan sub MAU 13229* (*carpol. coll. 187*) (MAU, 2 sheets); upland climax forest of Macabé, 24 Nov. 1938 (st), *Wiehe sub MAU s.n.* (MAU). MONTAGNE COCOTTE: degraded forest, 2,200 ft. (760 m), 8 Nov. 1969 (fr), *Barclay 1693* (K); on crest, 9 Nov. 1969 (fr), *Guého sub MAU 14192 (carpol. coll. 186)* (MAU); degraded forest on summit, 770 m, 1 Dec. 1978 (fl), *Lorence 1978* (MO); 4 Jan. 1979 (fl), *Lorence 2250* (K, MAU, MO, P); *Lorence 2251* (K, MAU, MO, P, REU, Z). WITHOUT PRECISE LOCALITY: 1865 (fl), *De Franqueville s.n. sub Herb. DeCandolle 16, 2: 660, no. 12* (G-DC; microfiche, MO); (fl), *Anon. sub Herb. Richard s.n.* (P); (fr), *Vaughan V 35 sub MAU spirit coll. 52* (MAU).

Tambourissa sieberi seems to be most closely related to *T. bathiei* from Madagascar, particularly in terms of floral morphology, which is discussed under the latter species. Both belong to species Group 6. Among Mauritian species, *T. sieberi* shares several features with *T. quadrifida,* including cauliflory, a thyrsic inflorescence structure, closed gynoecious floral receptacles which open by small apical pores, and similar strong, fermenting-fruity floral odors. *Tambourissa quadrifida* is totally glabrous, however, and appears to be more closely allied to the Madagascan *T. perrieri* (Group 7) than to *T. sieberi.*

A sterile collection of *Tambourissa* from northern Madagascar (*Baron 6720,* K) with similarly tomentose leaves, accompanied by a pencil sketch of a solitary, terminal fruit, apparently represents an undescribed species possibly allied to *T. sieberi.* Besides having solitary, terminal fruits, the leaves of *Baron 6720* differ from those of *T. sieberi* in containing numerous oil cells in the lamina and in having less densely branched ultimate veins. It is described as *Tambourissa* "sp. D" (no. 43) at the end of this treatment.

Flowers of *Tambourissa sieberi* are either bright yellow or dark purple, often within the same population. Floral odor in both sexes is strong and cloying, reminiscent of overripe or fermenting fruit.

Vernacular name. Bois tambour (Mauritius).

31. **Tambourissa bathiei** Cavaco, Bull. Soc. Bot. France 104: 284, fig. 1. 1957; Cavaco in Humbert, Fl. Madagascar 80: 20, fig. V:2–5. 1959. TYPE: Madagascar. Majunga: Firingalava, right hand tributary of the Ikopa River, W of Antsiafabositra (probably July 1899) (fl), *Perrier de la Bâthie 495-A* (holotype, P).

Monoecious tree, the new growth hirsute. Leaves (known only from the inflorescence) presumably opposite, petiolate; petioles 5–6 mm by 0.8 mm, hirsutulous; lamina chartaceous, elliptic, 40–58 mm by 20–25 mm, the apex shortly acuminate, the base acutely cuneate, the secondary veins 5–7 pairs, making a 65–70° angle with the costa, the venation prominent, visible to 4° on both surfaces, the margin plane. Inflorescence cauliflorous, unisexual, a condensed pleiochasium, or thyrse of (8–)20–34 flowers, sometimes leafy, the floral axis (20–)55–95 mm long by 3–4 mm wide medially, hirsutulous-pubescent. Androecious flower in bud globose, 10–13 mm diam., sparsely pubescent, apiculate with 3–4 minute, obtuse velutinous tepals, the pedicel 25–45 mm by 1.5–2 mm, subtended by a small, caducous ciliate deltoid bracteole 2 mm long; at anthesis deeply 3–4-fid, 25–35 mm diam., the lobes spreading ± flat; stamens numerous, ca. 350–450, clavate, 2–3 mm long by 1–1.5 mm wide, the filament well developed, comprising ca. ½–⅔ total length of stamen, the loculi apical, connivent or confluent at the obcordate-emarginate apex, occupying ca. ⅓–½ total length of stamen, the internal receptacle surface with clusters of short, dense hairs between the stamens. Submature gynoecious inflorescence a fulvous, velutinous-pubescent condensed pleiochasium of 8 flowers, the floral axis 24 mm by 2.5 mm. Submature gynoecious flower in bud globose, 7–8 mm diam., apiculate with 3–4 obtuse, velutinous tepals, the pedicel 12–15 mm by 1.5 mm; styles numerous, several hundred, completely lining the receptacle, narrowly conical, 1 mm long by 0.3–0.4 mm wide at the slightly ventricose base, the acuminate apex slightly papillose, the internal receptacle surface densely velutinous between the styles. Mature gynoecious flowers, fruiting receptacle, and carpels unknown.

Distribution. Endemic to Madagascar (Fig. 30).

Habitat. *Tambourissa bathiei* is known only from the type, which was collected along the Ikopa River, probably in riverine forest, in the Majunga province of western central Madagascar. The area formerly supported semideciduous dry forest of *Dalbergia* and *Commiphora,* but is now mainly savannah due to human disturbance.

On the basis of floral morphology, *Tambourissa bathiei* appears to be most closely related to *T. sieberi,* a species endemic to Mauritius, which also belongs to Group 6. Both species have small leaves, densely pubescent new growth, are cauliflorous with yellowish velutinous, generally unisexual thyrses or pleiochasia, and globose gynoecious receptacles lined with numerous narrowly conical styles.

Although mature gynoecious flowers of *Tambourissa bathiei* are unknown, the buds are similar to those of *T. sieberi,* which open by a small, subentire apical pore only 1–2 mm diam. Androecious flowers of *T. bathiei* have numerous clavate stamens with long, distinct filaments and loculi connivent or confluent at the obcordate apex. In contrast, stamens of *T. sieberi* are broadly deltoid-ovate, sessile, and have separate lateral loculi along most of their length. Further collections, particularly mature gynoecious flowers and fruit, of this poorly known species are required. See discussion under species number 42.

32. **Tambourissa perrieri** Drake in Grandidier, Hist. Phys. Madagascar 1(1): 24. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911; Cavaco in Humbert, Fl. Madagascar 80: 30, fig. VIII:5–7. 1959. TYPE: Madagascar. Majunga: vicinity of Maevatanana, Ampassiri, 15 July 1899 (fl), *Perrier de la Bâthie 495* (holotype, P; isotypes, P, 2 sheets).

Monoecious shrub or tree 2–8 m tall, the bark smooth, dark, the branches spreading, the new growth sparsely pilose, glabrescent, the mature leafy stems pale green, smooth, glabrous, 2–2.5 mm diam. Leaves opposite, petiolate, glabrous; petioles 5–10(–20) mm by 1–2 mm; lamina chartaceous to subcoriaceous, both surfaces slightly lustrous, narrowly elliptic, narrowly ovate to narrowly oblong, 75–250(–280) mm by 27–50(–75) mm, the apex acuminate, the base acute to slightly obtuse, the secondary veins 7–13 pairs, making a 75–85° angle with the costa, the venation very prominent, finely reticulate, visible to 4(–5°) on both surfaces, the margin plane. Inflorescence cauliflorous on meristematic swellings on the trunk, ramiflorous or rarely terminal, a short, unisexual or sexually mixed pleiochasium of 7–9 flowers, the floral axis glabrous or with scattered hairs, 55–125 mm by 2–4 mm, each pedicel subtended by a broadly deltoid, ciliate bracteole. Androecious flower in bud globose, 9–11 mm diam., smooth, glabrous or with rare, scattered hairs, apiculate with 4 small, thick hirsutulous deltoid tepals, the pedicel 10–32 mm by 1–1.5 mm, with scattered hairs; at anthesis deeply 4-fid, 18–25 mm diam., the lobes spreading flat; stamens numerous, ca. 150–200, ovoid to obovoid or clavate, 1.8–3 mm long by 1.2–1.5 mm wide, more or less recurved, subsessile or the filament comprising up to ½ total length of the stamen, the loculi confluent at the obtuse apex or separate, the connective retuse, not prolonged, the internal receptacle surface with scattered to clustered short, simple hairs between the stamens. Gynoecious flower in bud obovoid to obpyriform, 9–11 mm long by 6–7 mm wide, ± glabrous or with a few hairs basally, apiculate with 4–5 small, thick hirsutulous deltoid tepals, the pedicel stout, tapered, 3–15 mm by 1.5–2 mm wide medially; at anthesis obovoid to obpyriform, 12–14 mm long by 7–9 mm wide, the apex shallowly 4–5-fid, the lobes thick, erect, deltoid, the orifice 3–6 mm diam., comprising ca. ½ total width of the receptacle; styles numerous, ca. 200, crowded, shortly conical, 5-angled, 0.5–0.7 mm long by 0.5 mm diam. at the slightly ventricose base, the apex shortly acuminate, the internal receptacle surface densely velutinous with short, white hairs between the styles and on inner surface of the lobes. Fruiting receptacle solitary, borne on the trunk or branches, rarely terminal, obovoid, subglobose or rarely cupuliform, 50–150 mm long by 35–130 mm wide, externally grayish, corky, smooth or venose, the orifice comprising $\frac{1}{10}$–$\frac{1}{5}$ total width of fruit, the styles conical; pedicel and peduncle 28–45 mm by 6–10 mm. Mature carpels ovoid-compressed, 8–10 mm long by 7–8 mm wide, the endocarp brown.

Distribution. Endemic to Madagascar (Fig. 30).

Habitat. Tambourissa perrieri appears to be commonest in the northwestern sector of Madagascar (the Diego Suarez, Sambirano and Majunga regions) where it apparently occurs in vegetation types ranging from semideciduous sclerophyllous moist forest of *Uapaca*/Chlaenaceae and dry forest of *Dalbergia/Commiphora/Hildegardia,* frequently along rivers, to wet forest of *Tambourissa/Weinmannia.* As most collections lack precise data, it is often difficult or impossible to determine the exact habitat. In addition, two collections of what appear to be *T. perrieri* (but differ in having cupuliform fruits) are known from the lower limits of the *Tambourissa/Weinmannia* zone (ca. 900 m) of the eastern domain at Analamazaotra near Perinet, a seemingly disjunct distribution pattern possibly attributable to undercollecting.

MADAGASCAR. DIEGO SUAREZ: Manongarvio Massif W of Sambirano River, above 510 m, Apr. 1909 (fr), *Perrier de la Bâthie 10116* (P); Sambirano, Feb. 1923 (fr), *Perrier de la Bâthie 15465* (P). MAJUNGA: Bemarivo River Bassin, Boina, 300 m, Aug. 1907 (fl), *Perrier de la Bâthie 10125* (P); Mt. Bekolosy, near Maormandla, Mar. 1909 (fr), *Perrier de la Bâthie 10117* (P). TAMATAVE: near Analamazaotra, 800 m, 1912 (st), *Perrier de la Bâthie 10128* (P); Maromisaba, near Analamazaotra, 1,000 m, Feb. 1921 (fr), *Perrier de la Bâthie 15958* (P).

Morphologically, *Tambourissa perrieri* most closely approaches *T. quadrifida* from Mauritius, the only other member of Group 7. Both species are cauliflorous, rarely ramiflorous or terminal, with unisexual or sexually mixed pleiochasia or thyrses produced along most of the length of the trunk. Androecious flowers of both split deeply into four flat or recurved segments bearing numerous short stamens. The gynoecious flowers of both are obovoid to obpyriform or ellipsoid with a small orifice; it is much smaller (1–2 mm diam.) in *T. quadrifida* which also has thicker, obtuse or retuse leaves with more obscure venation. Both species occur in relatively dry habitats and form a group apparently not closely allied to other members of the genus, with the possible exception of Group 6.

Vernacular name. Ambora-lavaravina (Madagascar).

33. **Tambourissa quadrifida** Sonn., Voy. Ind. Oriental ed. 1, 2: 237, tab. 134. 1782; ed. 2, 4: 405, tab. 134. 1806; Gmel., Syst. Nat. 2(1): 16. 1791; A.DC., Prodr. 16(2): 658. 1868; Baker, Fl. Mauritius 288. 1877; Perk. & Gilg, Pflanzenr. 4, 101: 71. 1901, excl. synon. *T. obovata*; Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902, pro parte, excl. synon. *T. purpurea, T. rota, T. parvifolia*; Perk., Pflanzenr. 4, 101 (Nachtr.): 41. 1911. *Mithridatea quadrifida* (Sonn.) Comm. ex Schreb., Gen. Pl. 2: 783. 1791; Willd., Sp. Pl. 1(1): 27. 1797; Spreng., Syst. 5(3): 866. 1826. *Ambora quadrifida* (Sonn.) Poir., Encycl. 7: 565. 1806; Tabl. Encycl. 784. 1806; Tul., Monogr. Monim. 297. 1855. TYPE: Ile de France (Mauritius). Without precise locality (ca. 1775) (fl), *Commerson s.n. sub Herb. A. L. de Jussieu 16708* [lectotype, P-JUSS, here designated (photo, MO); isolectotypes, P-JUSS (photos, MO), both mixed with *T. elliptica* subsp. *micrantha*].

Ambora sempervirens F. G. Dietr., Lexic. Gart. 1: 342. 1802, nom. superfl., based on *T. quadrifida*.

A. tambourissa Lam. ex Steud., Nom. Bot. 37. 1821, nom. superfl., non *A. tamburissa* Boiv. ex Tul.

Mithradatea tamburissa Bojer, Hortus Maurit. 290. 1837, nom. superfl., based on *T. quadrifida*.

Ambora neglecta Tul., Monogr. Monim. 432. 1855. *Tambourissa neglecta* (Tul.) A.DC., Prodr. 16(2): 659. 1868; Perk. & Gilg, Pflanzenr. 4, 101: 71. 1901. TYPE: Mauritius. July 1855, *Labillardiere s.n.* (lectotype, P, here designated).

Monoecious to subdioecious tree attaining 15 m tall, the stems often multiple, to 15–30 cm D.B.H., the bark light brownish gray, flaking or checking, the new growth totally glabrous, the mature leafy stems glaucous, smooth to longitudinally striate, 2–4 mm diam. (suckers to 7–8 mm diam.). Leaves opposite to subopposite (sometimes alternate on suckers), petiolate, glabrous; petioles 5–12 mm by 1–1.5 mm; lamina subcoriaceous, broadly to narrowly elliptic, oblong or obovate, (30–)45–100 mm by (13–)17–52 mm, the apex shortly acute to mucronate, obtuse, rounded or retuse, the base acutely decurrent to acutely cuneate, the secondary veins 4–8 pairs, making a 55–65° angle with the costa, the venation ± obscure adaxially, visible to 2–3° on both surfaces, the margin plane to slightly revolute. Inflorescence a glabrous, generally ± unisexual, sometimes leafy, condensed pleiochasium or sparsely branching thyrse of (3–)5–35(–110) flowers, cauliflorous on meristematic swellings along the entire length of the trunk, or the flowers rarely solitary on leafless nodes or axillary, the floral axis (30–)40–180 mm by 2–4 mm, the flowers borne singly or in cymose units of 2–3. Androecious flower in bud smooth, obovoid to ellipsoid, 10–20 mm long by 7–10 mm wide, apiculate with 3–4 minute, glabrous, obtuse-deltoid tepals, the pedicel 10–30 mm by 1–1.6 mm, occasionally jointed to a distinct peduncle up to 12 mm long, often subtended by an obtuse, ciliate bracteole 0.5 mm long by 0.5–1 mm wide; at anthesis deeply (3–)4-fid, splitting deeply to the base, 20–32 mm diam., the lobes ultimately completely reflexed; stamens numerous, ca. 300–500, ellipsoid to oblong, 1.5–2.5 mm long by 0.8–1.4 mm wide, the filament distinct, comprising ca. ¼–⅓ total length of the stamen, the connective emarginate to slightly apiculate, the internal receptacle surface with scattered clusters of short hairs between the stamens. Gynoecious flower in bud obovoid to ellipsoid, 10–16 mm long by 7–10 mm wide, smooth, glabrous, apiculate with 3–4 minute deltoid tepals, the pedicel 7–10 mm by 1.5–2 mm, sometimes jointed to a peduncle attaining 10 mm long, often subtended by a minute bracteole; at anthesis with a subentire, shallowly 3–5-fid orifice 1–2 mm diam., the thick deltoid lobes straight or scarcely outcurved; styles numerous, ca. 200–300, lining the receptacle except near the apex, shortly conical, 0.4–0.6 mm long by 0.6 mm diam. at the abruptly swollen base, the internal receptacle surface velutinous between the styles and on the lobes, the dense hairs short, the external surface soon becoming corky. Fruiting receptacles borne on the trunk and major branches, solitary or in clusters of 2–3, irregularly obovoid-pyriform to globose-urceolate and depressed, 50–170 mm long by 50–100 mm diam., the walls 16–25 mm thick, externally corky brown, the orifice small, 5–10 mm diam., comprising ca. $\frac{1}{10}$ total width of fruit, the internal surface with numerous, scattered shortly conical styles 0.7–0.8 mm long by 0.3–0.4 mm wide basally, the pedicel and peduncle stout, 10–20 mm long by 7–18 mm diam. medially. Mature carpels ovoid-compressed, 13–19 mm long, 7–13 mm wide, 5–7 mm thick, the endocarp pale to dark brown, the surface minutely scrobiculate-rugose. Gametic chromosome number, $n = 19$.

Distribution. Endemic to Mauritius (Fig. 38).

Habitat. Tambourissa quadrifida is restricted to the western escarpments of the central plateau, ranging from the Trois Mamelles mountain range in the north to the mountains opposite Le Morne Brabant in the south. It is local and occasional to common in evergreen or semideciduous moist forest of *Elaeodendron orientale* Jacq., *Diospyros* spp., *Mimusops petiolaris* Dubard, and other species characteristic of the relatively dry rain shadow area. Although older trees of *T. quadrifida* are still relatively common, I observed no recent regeneration of the species, possibly due to grazing pressures from the high populations of stag which are maintained in the region for hunting.

MAURITIUS. CHAMAREL: Chamarel Hill, near first hairpin bend by roadside on edge of mountain reserves, 600 ft. (ca. 200 m), 19 Apr. 1939 (fl), *Vaughan V 1512* (MAU, 5 sheets); Chamarel, Dec. 1937 (st), *Vaughan 1512A* (MAU). PITON DU FOUGE: W flank, dry forest, ca. 400 m, 9 Aug. 1975 (fl), *Lorence 1337* (K, 2 sheets; MAU); flank of mountain ridge facing Le Morne Mt. and overlooking Coteau Raffin Village, 9 Aug. 1975 (fl), *Guého sub MAU 17356* (MAU). TROIS MAMELLES MT.: dense forest near Trois Mamelles, Aug. 1928 (fl), *Vaughan 544* (K). YEMEN MATALA VALLEY: under Brise Fer Mountain, dry forest (st), *Bernardi 14846* (G); 4 Dec. 1973 (fl), *Coode et al. 4270* (K, 2 sheets; MAU); W foothills of Brise Fer Mt., Yemen, Matala Valley, 17 Jan. 1976 (fr), *Lalouette sub MAU 17744* (MAU); 17 Mar. 1979 (fl, fr), *Lorence & Lalouette 2538* (K, MO, P, REU, Z); (fl), *Lorence & Lalouette 2539* (MO); 31 May 1979 (fl), *Lorence 2654* (K, MO, P, Z); (fl), *Lorence 2655* (K, MO, P); (fl), *Lorence 2656* (MO, REU); Yemen estate, 4 July 1968 (fl), *Maingard sub MAU 13266* (MAU); by side of road at Yemen, 4 July 1968 (fl, fr), *Vaughan sub MAU 13215 (carpol. coll. 178)* (MAU, 4 sheets). WITHOUT PRECISE LOCALITY: (st), *Anon. 4663* (G, K); (fl), *Anon. sub Herb. Delessert s.n.* (G); (fl), *Anon. sub Herb. DeCandolle 16(2): 658* (G-DC, 2 sheets; microfiche, MO); (st), *Anon. sub Herb. Richard s.n.* (P, left hand collections only); *Anon. sub Herb. Richard 111* (P, 2 sheets); (fl), *Ayres s.n.* (K); (fl), *Bojer s.n.* (K); 1831 (fl), *Bouton s.n.* (P); 1814 (fl), *Carmichael s.n.* (K); (fl), *Ilardwicke 6* (G); (st), *Martin s.n.* (G); (fl), *Martin 607* (G, 2 sheets).

Tambourissa quadrifida appears to be most closely allied to *T. perrieri* from Madagascar, also of species Group 7. The latter is distinguishable by its globose androecious flower buds, gynoecious flowers with larger orifices (3–4 mm diam.), longer, acuminate leaves with more prominent venation, and floral ground tissue with abundant oil cells lacking in *T. quadrifida.*

Living flowers produce a strong odor of ripe fruit similar to that of *Tambourissa sieberi.* Two floral color morphs occur in the population at Yemen, the androecious flowers being either tomato red or salmon orange, whereas the gynoecious flowers have either red or greenish white to pink styles. Buds and outer receptacle surfaces are marbled green, often flushed with red.

Vernacular names. Bois tambour, Pomme de singe (Mauritius).

34. Tambourissa alaticarpa Lorence, nom. nov. *Phanerogonocarpus perrieri* Cavaco, Bull. Soc. Bot. France 104: 613. 1957; Cavaco in Humbert, Fl. Madagascar 80: 4. 1959 non *Tambourissa perrieri* Drake in Grandidier, Hist. Phys. Madagascar 1(1): 24. 1902. TYPE: Madagascar. Tamatave: E coast, bank of the Fandrarazana River, 200 m, 1930 (fl), *Perrier de la Bâthie 10102* (holotype, P).

Monoecious treelet, the new growth pale yellowish villous, the hairs simple, the submature stems 3 mm diam., stramineate, villous. Leaves opposite, petiolate; petioles 15–16 mm by 2 mm, villous; lamina chartaceous, elliptic to oblong, 210–220 mm by 75–80 mm, the apex abruptly acuminate, the base cuneate, adaxially sparsely pilose, abaxially densely pilose, the costa velutinous, depressed adaxially, prominent abaxially, the secondary veins ca. 7 pairs, making a 50–60° angle with the costa, festooned brochidodromous, the venation raised and visible to 3–4° on both surfaces, the margin serrate-dentate with 9–10 pairs of narrowly acute, antrorse teeth ca. 1 mm long, the tips glandular, indurated. Apparently cauliflorous (also ramiflorous?), the inflorescence either a sexually mixed pleiochasium 150–250 mm long with 7–10 lateral androecious flowers and a single, terminal gynoecious flower, the floral axis 100–240 mm by 1.5–3 mm, pilose to velutinous, or a short, unisexual pleiochasium 20–30 mm long of 7–10 androecious flowers, the floral axis 6–20 mm by 0.5–1 mm, pilose to villous. Androecious flower in bud glabrous or with rare, scattered hairs, obovoid to ellipsoid, 4–5 mm by 3–3.5 mm, apiculate, the apex with 3–4 acute, scarious deltoid tepals 0.5 mm long and wide, the pedicel 13–19 mm by 0.5 mm, sparsely pilose, subtended by a subulate-linear bracteole 2–3 mm long; at anthesis deeply 4-fid, 7–9 mm diam., the lobes spreading flat; stamens ca. 38, clavate, 1.2–1.6 mm long by 0.7–0.8 mm wide, the filament distinct, stout, the loculi separate, lateral or oblique, occupying ¼–½ total length of the stamen, the connective obtuse or apiculate, scarcely or not prolonged, the internal receptacle surface glabrous. Gynoecious flower terminal, sparsely pilose or glabrate, in bud narrowly obovoid, tubular, 22–28 mm by 4–5 mm, angular with 4–6 longitudinal wings 1–1.5 mm wide running from apex to pedicel, the apex crowned by 6–8 subulate tepals 1–1.5 mm long, the wall ca. 0.5 mm thick, the pedicel scarcely differentiated, 20–25 mm by 1.5 mm diam. medially; at anthesis apparently opening by a small (ca. 1 mm diam.) apical orifice flanked by several deltoid lobes; styles numerous, ca. 250–300, sharply conical, 1 mm long by 0.5 mm diam. basally, acuminate, curved antrorsely, the internal apical portion of the receptacle velutinous with short, simple white hairs, the styles interspersed with short, dense hairs. Fruiting receptacle probably resembling that of *T. longicarpa* (i.e., cylindrical, narrowly winged), the fruiting carpels (fide Perrier de la Bâthie) embedded in the orange receptacular tissue, the mesocarp red, the endocarp black.

Distribution. Endemic to Madagascar (Fig. 24).

Habitat. Presumably from lowland wet forest of Myristicaceae/*Anthostema*, the species is known only from the type.

Along with *Tambourissa longicarpa*, *T. alaticarpa* comprises the very natural species Group 8, characterized by elongate, narrowly winged gynoecious flowers and fruits. It differs from the former species in having larger, more sparsely pubescent leaves with smaller, more numerous teeth (only 2–3 pairs in *T. longicarpa*), and externally sparsely pilose to glabrate buds and flowers.

35. Tambourissa longicarpa Lorence, nom. nov. *Phanerogonocarpus capuronii* Cavaco, Bull. Soc. Bot. France 104: 612, figs. 1–4. 1957; Cavaco in Humbert, Fl. Madagascar 80: 3, fig. I:1–6. 1959 non *Tambourissa capuronii* Cavaco, Bull. Mus. Hist. Nat. (Paris), Ser. 2, 29: 287. 1957. TYPE: Madagascar. Diego Suarez: Atondradama Pass, N of the Masoala Peninsula, E forest, ca. 500 m, 22 Dec. 1953 (fl, fr), *Capuron 8775-SF* (holotype, P).

Large monoecious treelet, the new growth pale yellowish villous, the hairs simple, the mature leafy stems fulvous velutinous, 2–3 mm diam. Leaves opposite, petiolate; petiole 10–13 mm by 1.5–2 mm, fulvous velutinous; lamina broadly elliptic, 75–105 mm by 43–65 mm, chartaceous, the apex deltoid, acute, the tip thickened, the base cuneate, the adaxial surface sparsely pilose, especially along the costa and veins, glabrescent, the abaxial surface densely pilose with pale yellowish white hairs, especially along the costa and veins, the costa depressed adaxially, prominent and rounded abaxially, the secondary veins 5–6 pairs, making a 45–55° angle with the costa, the basal pairs festooned brochidodromous, the apical ones often excurrent into the marginal teeth, the venation visible to 2° adaxially and to 3° abaxially, the margin slightly revolute, strongly dentate in the apical ⅓ with (1–)2–3 pairs of broadly deltoid teeth 3–5 mm long, the tips thickened, glandular. Inflorescence basally cauliflorous, produced on meristematic swellings from the trunk, either a sexually mixed, 15–22 flowered pleiochasium with 1–3 terminal gynoecious flowers, the androecious flowers lateral in opposite to subopposite pairs or cymose groups of 2–3, the floral axis velutinous, 70–95 mm by 1–1.8 mm, subtended by several deltoid bracteoles, or a smaller unisexual pleiochasium of 7–

9 androecious flowers, the floral axis 18–35 mm by 1 mm. Androecious flower in bud hirsute, globose, 4–5 mm diam., apiculate with 1(–2) pairs of minute, subulate-deltoid tepals 0.3–0.5 mm long, the pedicel 10–22 mm by 0.5 mm, pilose, subtended by a subulate-naviculate, pilose bracteole 1 mm long; at anthesis deeply 4-fid, 9–11 mm diam., the lobes spreading flat, ultimately reflexing, each bearing 2–3 minute, fleshy tepals apically within; stamens 40–50, subulate, 1.5–2.5 mm long by 0.8–1 mm wide, the filament distinct, thick, the loculi separate, lateral or abaxially ± unifacial, 1–1.5 mm long, occupying ca. ½ total length of stamen, the connective prolonged, acute to apiculate, the inner receptacle surface with scattered hairs between the stamens. Gynoecious flower in bud narrowly obconical, tubular, 30–35 mm by 3.5–4 mm, ± quadrangular with 4(–5) lateral longitudinal wings ca. 1 mm wide, fulvous hirsute-velutinous, the apex bearing 4–6 deltoid-subulate hirsute tepals 1–2 mm long, the receptacle wall ca. 1 mm thick, the pedicel tapered, scarcely differentiated from the receptacle, 20–25 mm by 1 mm, hirsute, subtended by 2 subulate bracteoles 2–3 mm long; at anthesis opening by 4 deltoid lobes, the orifice ca. 1 mm diam.; styles numerous, ca. 500, crowded, conical, 0.4–0.5 mm long by 0.3 mm wide basally, the base slightly ventricose, the internal receptacle surface apically velutinous, the cavity ca. 2–2.5 mm diam., the styles interspersed with numerous short hairs, a mucilaginous exudate present. Fruiting receptacle pendulous, cylindrical-ellipsoid, 160 mm by 70 mm, externally pale corky brown, bearing 4–5 longitudinal wings, 4–5 mm wide, the orifice narrow, at maturity splitting lengthwise and exposing the central tube bearing part of the carpels, the pedicel and peduncle ca. 120 mm by 6 mm. Mature carpels ovoid-compressed, 12 mm by 5–6 mm, the mesocarp thin, red-orange, fleshy, the endocarp brown, minutely foveolate.

Distribution. Endemic to Madagascar (Fig. 24).

Habitat. The type and only known collection is from the eastern lowland Myristicaceae/*Anthostema* wet forest zone.

Most closely allied to *Tambourissa alaticarpa,* the only other member of species Group 8, *T. longicarpa* differs by its smaller leaves with fewer, much larger teeth, its more densely villous inflorescence and flowers, and by its stamens with the connective prolonged beyond the anther. Further collections and field studies are greatly desired.

36. Tambourissa castri-delphinii Cavaco, Bull. Soc. Bot. France 104: 283. 1957; Cavaco in Humbert, Fl. Madagascar 80: 32, fig. IX:9–10 (non fig. VIII). 1959. TYPE: Madagascar. Tulear: Ebakika, Fort Dauphin district, in secondary forest (savoka), small tree, 17 Nov. 1932 (fl), *Decary 11052* (holotype, P).

Small monoecious or subdioecious trees 5–7 m tall, the mature leafy stems terete to subtrigonous, 3–7 mm diam., glabrous, stramineate. Leaves ternate, rarely opposite, petiolate, glabrous; petioles 7–13 mm by 1.5–2 mm; lamina subcoriaceous, both surfaces moderately lustrous, ovate to oblong, 88–170 mm by 38–68 mm, the apex abruptly and shortly acuminate, the base acutely cuneate, the secondary veins 5–7 pairs, making a 45–50° angle with the costa, the venation raised and prominent, visible to 4° on both surfaces, the margin thickened, slightly revolute. Androecious inflorescence ramiflorous, axillary on the leafless nodes, a contracted pleiochasium or fascicle of 4–9 flowers, the floral axis 1–9 mm by 1.5–2 mm, sparsely puberulent basally, subtended by several pale, naviculate-deltoid, ciliate bracteoles 0.5–1.5 mm long. Androecious flower in bud glabrous, globose, 9–18 mm diam., apiculate with 4–6 short, obtuse tepals, the pedicel 10–18 mm by 0.8–1 mm, subtended by a bracteole; at anthesis deeply 4–5-fid, 25–32 mm diam., the lobes spreading flat, reflexing, purple within; stamens numerous, ca. 200–300, ovoid to deltoid, thin, 2.5–4 mm long by 1.5–2 mm wide, the filament short, subsessile, the loculi lateral, confluent at the obtuse apex, rarely free, the connective not prolonged, the internal receptacle surface with scattered or clustered simple hairs between the stamens. Gynoecious flowers presumably ramiflorous like the male, at anthesis napiform-depressed, 4–6 mm long by 10–14 mm diam., externally glabrous, internally densely hirtellous on the lobes, the orifice small, X-shaped, the styles numerous, ca. 800–900, conical acuminate, 0.7–0.9 mm long and wide basally, interspersed with numerous hairs; pedicel and peduncle 8 or more mm long. Mature fruiting receptacle subglobose-cupuliform, 40–45 mm long by 40–60 mm wide, externally corky, the walls 10–12 mm thick, the orifice comprising ca. ¼–½ total width of fruit, the styles conical 0.8–1.5 mm by 0.8 mm, interspersed with rare hairs; pedicel and peduncle 17 mm by 5 mm. Mature carpels ovoid-compressed, 10–11 mm by 5–8 mm, pale tan.

Distribution. Endemic to Madagascar (Fig. 30).

Habitat. Tambourissa castri-delphinii is known only from the SE coastal region between Mananjary and Fort Dauphin. Capuron notes that the species occurs in coastal "savoka" (secondary or disturbed primary forest) over old sand dunes.

MADAGASCAR. FIANARANTSOA: Mananjary, Mar.–Apr. 1909 (fr), *Geay 8287* (P). TULEAR: between Fort Dauphin and Manantenina, near Manambato (fl), *Capuron 28667-SF* (P); Ebakika, 18 Nov. 1932 (fl), *Decary s.n.* (P); Mendena, 16 Feb. 1949 (fr), *Capuron 378-SF* (P); Fort Dauphin, Manambato, 12 Dec. 1972 (fl), *Jacquenim 1197* (P).

Cavaco (1957b) states that *Tambourissa castri-delphinii* is related to *T. religiosa,* also Madagascar, because leaves of both species are similarly subcoriaceous or coriaceous with prominent venation. This similarity is most likely because both species occupy a similar habitat in coastal forest. More significantly, adult phyllotaxis is different, being opposite in *T. religiosa* and usually ternate in *T. castri-delphinii,* the latter character otherwise found only in *T. ficus* and *T. peltata,* both Mauritian endemics. In addition, venation of all three ternate-leaved species is prominent and finely reticulate, showing a high degree of organization. Furthermore, androecious flowers of *T. religiosa* and *T. castri-delphinii* are totally different. Both *T. peltata* and *T. castri-delphinii* are cauliflorous or ramiflorous on the upper branches, producing large, deeply 4(–5)-fid androecious flowers with recurved segments and numerous, broadly ovoid to deltoid subsessile stamens, whereas those of *T. religiosa* are small and globular with fewer, much smaller stamens. For these reasons *T. peltata* and *T. castri-delphinii* appear to be more closely related and I have placed them together in species Group 9.

Tambourissa peltata differs from *T. castri-delphinii* by its larger, solitary or paired androecious flowers with thicker pedicels, and discoid female receptacle with broad, sterile lobes and columnar styles. Gynoecious flowers of *T. castri-delphinii* differ from both *T. ficus* and *T. peltata* in having an X-shaped orifice.

37. Tambourissa ficus (Tul.) A.DC., Prodr. 16(2): 659. 1868; Perk. & Gilg, Pflanzenr. 4, 101: 69, fig. 18Q. 1901; Perk., Gatt. Monim. fig. 34Q. 1925. *Ambora ficus* Tul., Ann. Sci. Nat. (Paris) 4(3): 30. 1855; Tul., Monogr. Monim. 300. 1855. TYPE: "Java" (probably Mauritius). Without precise locality (ca. 1800) (fl), *Leschenault de la Tour s.n.* (holotype, P).

Ambora alternifolia Tul., Ann. Sci. Nat. (Paris) 4(3): 31. 1855; Tul., Monogr. Monim. 305. 1855. *Tambourissa alternifolia* (Tul.) A.DC., Prodr. 16(2): 660. 1868; Baill., Adansonia, Ser. 1, 9: 131. 1868–1870; Perk. & Gilg, Pflanzenr. 4, 101: 72. 1901; Cavaco, Bull. Soc. Bot. France 104: 284. 1957. TYPE: Ile Maurice (Mauritius). At the foot of the Pouce, above the plain at Moka, Oct. 1849, *Boivin s.n.* [lectotype, P, here designated, as to androecious floral buds only, excluding the stem and leaves which are *Homalium integrifolium* (Lam.) Baill. (Flacourtiaceae)].

Ambora obovata Tul., Ann. Sci. Nat. (Paris) 4(3): 31. 1855; Tul., Monogr. Monim. 306. 1855. *Tambourissa obovata* (Tul.) A.DC., Prodr. 16(2): 660. 1868; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901. TYPE: Ile Maurice (Mauritius). Woods of the Pouce, Sept. 1849, *Boivin s.n.* (holotype, P).

T. elliptica sensu Baker, Fl. Mauritius 288. 1877; sensu Perk., Pflanzenr. 4, 101 (Nachtr.): 44. 1911 non (Tul.) A.DC.

Ficus sapotoides Baker, Fl. Mauritius 284. 1877. TYPE: Mauritius. Pouce above plateau, Sept. 1862, *Ayers s.n.* (holotype, K; photo, P).

Monoecious to subdioecious treelet or tree 10–15 m tall and 10–15 cm D.B.H., the base of the trunk frequently swollen, the new growth finely pilose to fulvous tomentose, the mature leafy stems glabrous, stramineate, subterete, 2–5 mm diam. Leaves ternate to subalternate, rarely opposite to subopposite, petiolate, glabrous; petioles 10–25 mm by 1.5–2 mm (to 45 mm long on vigorous suckers); lamina chartaceous to subcoriaceous, broadly to narrowly obovate, oblanceolate, narrowly to broadly elliptic, 60–150 (–180) mm by (20–)30–75 mm (to 170 mm by 100 mm on vigorous suckers), the apex acuminate, acute, obtuse or retuse, the base acutely decurrent to acutely cuneate, the secondary veins 5–8(–11) pairs, making a 50–70° angle with the costa, the venation finely reticulate, prominent, visible to 3–4° adaxially and to 4° abaxially, the margin plane to slightly revolute; juvenile and sucker leaves often heterophyllous, the petioles red when living, the lamina apically serrate-dentate with 1–3 pairs of teeth. Inflorescence cauliflorous on the swollen base of the trunk, sometimes extending up the lower portion of the trunk for several meters or rarely on the leafless parts of the lower branches, the flowers solitary or in fascicles of 2(–3) on the meristematic swellings. Androecious flower in bud globose-depressed to napiform-depressed, 20–30 mm diam. by 15–25 mm long, pubescent, smooth to corky, longitudinally ribbed basally, the walls thick and fleshy, apiculate with 3–5 minute, hirsute tepals, the pedicel stout, tapered, jointed near the base, the pedicel and peduncle 15–25 mm by 3–4.5 mm diam. medially, pubescent to velutinous, bearing several hirsute, subulate-naviculate bracteoles 1–2 mm long; at anthesis shallowly to deeply 4–6(–7)-fid, either partially closed and urceolate, 20–40 mm diam. by 17–30 mm long, or the lobes spreading flat open, 35–75 mm diam.; stamens very numerous, ca. 900–1,800, curvate, linear to ellipsoid or ligulate, 3–6 mm long by 0.5–1 mm wide, the filament basally thickened, comprising ¼–⅓ total length of the stamen, the loculi separate, parallel, lateral, or abaxially ± unilateral and extrorse, comprising ca. ⅓ total length of the stamen, the connective thick, apically prolonged, obtuse to apiculate or acute, comprising ca. ¼–⅓ total length of the stamen, the internal receptacle surface with clusters of simple hairs between the stamens. Gynoecious flower in bud napiform-depressed, thick, fleshy, the size and pubescence as in the androecious bud; at anthesis urceolate-napiform, 30–40 mm diam. by 15–30 mm long, externally corky brown, sparsely puberulent, the orifice ca. 15–25 mm diam., comprising ca. ⅔ total width of the receptacle, the 6–8 thick, deltoid lobes incurved; styles very numerous, ca. 1,000–2,000, narrowly conical or setose, 1.5–5 mm long by 0.3–0.5 mm wide basally, the sides longitudinally furrowed, the internal receptacle surface densely velutinous between the styles. Fruiting receptacle solitary at the base of the trunk, irregularly cupuliform, often ± compressed dorsally, 40–85 mm long, 135–175 mm wide, the orifice subentire, 90–130 mm wide, comprising ca. ⅔–¾ total width of the receptacle, the walls 10–16 mm thick, both surfaces corky brown, internally with numerous, setose styles 1.5–4.5 mm long by 0.5–0.8 mm wide basally, the pedicel and peduncle 20–65 mm long by 9–10 mm diam. medially. Mature carpels ovoid-compressed, 10–14 mm long, 5–7 mm wide, 4–6 mm thick, the endocarp dark brown, the surface scrobiculate.

Distribution. Endemic to Mauritius (Fig. 38).

Habitat. Tambourissa ficus is fairly widespread in mid to upper elevation wet and cloud forest formations (ca. 600–800 m), often forming localized populations near the summits of mountains or along rivers and lakes.

MAURITIUS. BAMBOU MOUNTAIN: top of Bambou Mt., 7 Oct. 1962 (fl), *Mulnier sub MAU s.n.* (MAU). BASSIN BLANC: forest inside Bassin Blanc Crater, 4 Nov. 1967 (fl), *Guého sub MAU 13228* (MAU); lower montane rain forest inside crater, 550 m, 21 Dec. 1978 (fr), *Lorence 2188* (K, MAU); (fl), *Lorence 2189* (MO); (fl, fr), *Lorence 2190* (MO); ca. 2 m from outside of lake, S side, 500 m, 25 May 1976 (fr), *Richardson et al. 4164* (K, MAU, MO); indigenous forest, 13 Mar. 1971 (fr), *Staub sub MAU 19283* (MAU). BRISE FER: 200–300 yards before summit of Piton Brise Fer, 29 Dec. 1966 (fl), *Guého sub MAU 12505* (MAU, 2 sheets); (fl), *Guého sub MAU 12509* (MAU); Brise Fer Mt., 609 m, July 1960 (fr), *Lalouette sub MAU 10020* (*carpol. coll. 111*) (MAU, 2 sheets); 20 Aug. 1966 (fr), *Lalouette sub MAU 12194* (*carpol. coll. 158*) (MAU); mature evergreen forest transitional to dry forest, 600 m, 8 Dec. 1978 (fl), *Lorence 2114* (MO); (fl), *Lorence 2115* (MAU, MO); (st), *Lorence 2116* (MO); (st), *Lorence 2117* (MO); a few hundred yards before reaching the summit of Brise Fer, 1 Oct. 1964 (fr), *Vaughan sub MAU 11429* (*carpol. coll. 154*) (MAU); (st), *Vaughan sub MAU 11430* (MAU); (fl), *Vaughan sub MAU 12505* (*spirit coll. 167*) (MAU). CROWN LAND DANGUET: near Port Louis, 4 Sept. 1947 (st), *Vaughan V 3177* (MAU). MACABÉ FOREST: ravines of Black River Gorges near Macabé, 28 Nov. 1950 (fl), *Duljeet FD 105* (*spirit coll. 41*) (MAU, 2 sheets); Macabé forest, near kiosk, transitional wet forest, ca. 660 m, 16 Dec. 1978 (st), *Lorence 2155* (MAU); (st), *Lorence 2156* (MO); Plateau Colophane below Macabé, ca. 600 m, 15 Jan. 1979 (st), *Lorence 2952* (MO); Macabé, near screen, 10 Dec. 1938 (st), *Vaughan sub MAU 1336A* (MAU); Macabé forest transect, 11 Aug. 1937 (st), *Vaughan 27 sub MAU 2359* (MAU); Macabé climax forest near large "natte" tree in plot, 16 Nov. 1967 (fl), *Vaughan sub MAU 13055* (MAU). MT. COCOTTE: degraded forest, 2,200 ft. (ca. 760 m), 8 Nov. 1969 (fl), *Barclay 1692* (K); dense indigenous thicket along crest, 8 Nov. 1969 (fl), *Guého sub MAU 14108* (MAU); low cloud forest with *Nuxia*, invaded by exotics, N slope, ca. 700 m, 19 Dec. 1978 (fl), *Lorence & Lecordier 2162* (K, MO); near summit, 770 m, 19 Dec. 1978 (fl), *Lorence & Lecordier 2163* (MO, P); forest of St. Marie near Mt. Cocotte, high forest, Nov. 1937 (fl), *Wiehe sub MAU 1511* (*spirit coll. 45*) (MAU). MT DEUX MAMELLES: degraded wet forest invaded by exotics, 630 m, 22 Jan. 1979 (st), *Lorence 2303* (MO). MT LAGRAVE: low forest on slopes, much invaded, 5 Apr. 1974 (fr), *Coode 5034 sub MAU 17598* (K, MAU). PIETER BOTH MT. RANGE: S flank below "La Fenêtre," totally degraded wet forest, ca. 550 m, 29 Sept. 1978 (st), *Lorence 1833* (MO). PITON DU MILIEU: dense indigenous thicket, rocky ridge at foot of the mountain, 25 Oct. 1969 (fl), *Guého sub MAU 14181* (MAU); low native thicket halfway up steep summit, 24 Nov. 1971 (fl), *Guého sub MAU 14983* (MAU); degraded lower montane wet forest, 650–750 m, 29 Dec. 1978 (st), *Lorence 2235* (MO); (st), *Lorence 2236* (MO). PITON DU FOUGE: E slopes, ca. 500 m, 27 Apr. 1976 (st), *Richardson et al. 4042* (K). POUCE MT.: shoulder of Le Pouce, Dec. 1860 (fl), *Ayres s.n.* (K);

shoulder of Le Pouce, Nov. 1862 (fl), *Ayres s.n.* (K); (st), *Boivin s.n.* (P, mixed with *T. pedicellata*); lower montane wet forest invaded by exotics, grading into cloud forest near summit, 600–700 m, 14 Dec. 1978 (st), *Lorence 2142* (MO); (fl), *Lorence 2143* (MO); 750–800 m (fl), *Lorence 2144* (K, MAU). RIVIÈRE DES GALETS: below Cascade 500 Pieds, 350 m, forest along river bank, 8 Nov. 1975 (fl), *Lorence 1485* (K, 2 sheets; MAU); Valley of Cascade 500 Pieds, *Calophyllum* wet forest, 550 m, 22 Dec. 1978 (st), *Lorence 2193* (MO). TAMARIN FALLS RESERVES: 518 m (fl), *Vaughan sub MAU 1509* (MAU). VUILLEMAN FOREST: near Midlands (fl), *King sub MAU 1765* (MAU). WITHOUT PRECISE LOCALITY: (fl), *Anon. sub Herb. Richard s.n.* (P, 2 sheets); common in forests of medium altitude (st), *Vaughan sub MAU 1513* (MAU).

Although one of the most polymorphic Mauritian species, *Tambourissa ficus* is nevertheless distinct from all other Mascarene species, and is the only one with flowers and fruit produced on the swollen base of the trunk. It is potentially monoecious [e.g., *Wiehe 1511* (MAU), *Vaughan sub MAU 12505* (MAU), *Lorence 2162* (MAU, MO)] but frequently produces flowers of a single sex. Although only four to eight flowers are produced during a single season per plant, this paucity has been compensated for by a floral gigantism unrivalled in the genus and indeed the entire family! Fully expanded androecious flowers may attain 60–75 mm diam. with the entire surface covered by ca. 900–1,800 stamens, whereas gynoecious flowers are large, urceolate cups 30–40 mm diam. lined with a comparable number of styles. The cupuliform fruits, which attain 175 mm diam., are also some of the largest in the genus.

Both foliar and floral morphology are variable in *Tambourissa ficus,* but are relatively constant within a given population. For example, populations from the central (Le Pouce Mt., Piton du Milieu) and western (Piton Brise Fer) mountain ranges have broadly elliptic to obovate, acute to obtuse leaves, hence the specific epithet *obovata* given by Tulasne. Those from the southern edge of the central plateau (Bassin Blanc, Mt. Cocotte, Rivière des Galets) tend to have narrower, elliptic to oblanceolate, acute to acuminate leaves. Such variation may occur within a single population, however, e.g., at Macabé forest.

Variation in floral morphology is expressed in length of stamens and styles, and form and color of androecious flowers. Populations from Bassin Blanc and Rivière des Galets, which grow along river and lake banks, have shorter styles and creamy white, urceolate androecious flowers that tend to split only about halfway open. Populations from mountain summits (e.g., Le Pouce and Piton Brise Fer) have pinkish to reddish purple androecious flowers that split completely open into a star shape and the gynoecious flowers have longer styles. Flower color and size and shape of stamens and styles are similarly variable in other species, e.g., *T. tau* and *T. quadrifida.* These floral and foliar differences intergrade gradually in *T. ficus,* making it impossible to formally recognize infraspecific taxa. For example, the Bassin Blanc population has androecious flowers and styles that are transitional between the Rivière des Galets and Brise Fer forms. As such, they are best recognized as variants of a single, polymorphic species.

In view of this variation, it is not surprising that *Tambourissa ficus* has been described as three distinct species of *Ambora* by Tulasne (1855a). He based *A. obovata* on a single sterile, leafy twig from Le Pouce and based *A. alternifolia* on a mixed collection consisting of androecious buds of *T. ficus* and leaves of *Homalium* (Flacourtiaceae). Furthermore, because the type of *A. ficus* consists of leaves and gynoecious flowers of the narrow-leaved form, which moreover was supposed to have been collected in Java, it is understandable that Tulasne described it as another species. He was apparently unaware that J. Leschenault de la Tour first visited Mauritius, where he apparently collected the type of *A. ficus,* before continuing on to Java (Steenis-Kruseman, 1950). *Tambourissa* is unknown from Java, and the locality on the label is evidently erroneous (Perkins, 1911).

I have lectotypified *Tambourissa alternifolia* on the basis of the large, solitary ficiform androecious flower buds with characteristic ligulate, apiculate stamens obviously belonging to *T. ficus.* I recognize the leaves as belonging to a Mascarene species of Flacourtiaceae [*Homalium integrifolium* (Lam.) Baill.] also occurring on Le Pouce Mt. Its leafy stem is minutely lenticellate, unlike any *Tambourissa* known to me, and furthermore the leaves lack the oil cells characteristic of Monimiaceae (Perkins & Gilg, 1901), a fact ignored by Cavaco (1957b).

Baker (1877) wrongly referred material of *Tambourissa ficus* from Le Pouce to *T. elliptica.* More surprisingly, he described comparable material of the same species, also from Le Pouce, as *Ficus sapotoides,* suggesting he failed to dissect flower buds and also overlooked the absence of stipule scars on the stem. Of the three available concurrently published names, I have retained

T. ficus because the type is the most complete, with both androecious and gynoecious flowers and leaves.

Tambourissa ficus belongs to the small species Group 9, also including *T. peltata* (Mauritius) and *T. castri-delphinii* (Madagascar). The ternate to subalternate leaf condition of these species appears to be derived, as seedlings and suckers of *T. ficus* and *T. peltata* have opposite leaves. *Tambourissa ficus* is most closely allied to *T. peltata* in leaf morphology but its leaves are thinner and generally lack the bright yellow-green tinge characteristic of *T. peltata*, and the stems are more slender. In addition, *T. ficus* is monoecious, usually basally cauliflorous, and has much larger flowers with more numerous parts. Furthermore, its gynoecious flowers are urceolate with setose styles as opposed to those of *T. peltata*, which are flat and discoid with columnar styles and produce a thick, mucilaginous exudate. With respect to gynoecious floral morphology, *T. ficus* more closely approaches Group 5, thus linking the two groups.

Vernacular names. Bois tambour, Pot de chambre jacot (Mauritius).

38. Tambourissa peltata R. Br. ex Baker, Fl. Mauritius 288. 1877; Perk. & Gilg, Pflanzenr. 4, 101: 71. 1901. TYPE: Mauritius. Without precise locality, 1814, *Carmichael s.n.* (lectotype, K, here designated, as to gynoecious collection only).

Dioecious treelet or tree 12–15 m tall and 30–40 cm D.B.H., the outer bark smooth, pale brown, longitudinally fissured, the new growth glabrous, the mature leafy stems smooth, stramineate, 3–7 mm diam., angled or subterete. Adult leaves ternate to subalternate, petiolate, glabrous; petiole 12–25 mm by 1–2 mm; lamina subcoriaceous to coriaceous, broadly to narrowly obovate, oblanceolate, elliptic, broadly elliptic or rarely ovate, 60–150(–180) mm by 30–70(–85) mm (reaching 225 mm long on vigorous suckers), the apex acuminate to acute, frequently obtuse or retuse, the base acutely cuneate to acutely decurrent, the secondary veins 6–9(–12) pairs, making a 55–65° angle with the costa, the venation very prominent and finely reticulate, visible to 4° on both surfaces, the margin slightly revolute; seedling and sucker leaves opposite, heterophyllous, the petiole red when living, the lamina oblanceolate to narrowly oblanceolate, with 1–3 pairs of short teeth apically. Inflorescence ramiflorous on the leafless branches or upper portions of the trunk, rarely axillary or on short, leafy shoots, the flowers solitary or in fascicles of 2–3. Androecious flower in bud glabrous, globose to ellipsoid, 10–14 mm diam. by 12–18 mm long, apiculate with 5–6 small, acute glabrous tepals, the pedicel and peduncle 6–20 mm by 1.5–3 mm, bearing few to many deltoid-naviculate, ciliate bracteoles to 1.5 mm long; at anthesis deeply 4–6(–7)-fid, 30–50 mm diam., the thick lobes ultimately reflexing; stamens numerous, ca. 200–400, ovoid-deltoid to linear-lanceolate, 4–7 mm long by 1.5–3 mm wide, the filament short or subsessile, the loculi separate or confluent apically, occupying almost entire length of the stamen, the connective broad, slightly prolonged or not, the internal receptacle surface glabrous, rarely with scattered hairs. Gynoecious flower in bud glabrous, broadly napiform-depressed, 14–17 mm diam. by 7–9 mm long, apiculate with 4 minute tepals, the pedicel and peduncle 6–12 mm by 2 mm, bracteolate as in androecious flower; at anthesis deeply 4–7-fid, 23–30 mm diam., the deltoid lobes ultimately reflexing, their internal surface ± verrucose-wrinkled, the receptacle discoid, flat to ± concave, the peltate central portion 13–16 mm diam., pubescent around the margin and between the styles; styles numerous, ca. 400–500, crowded and coalescent, virtually indistinguishable, columnar, 4–6-sided, 0.3–0.5 mm long by 0.3–0.4 mm diam., the apex flat to depressed, the gynoecium covered with a mucilaginous exudate. Fruiting receptacle solitary on the old stems or rarely on the upper part of the trunk, sometimes produced in large numbers, cupuliform, patelliform or discoid-peltate, 40–130 mm diam. by 15–60 mm long, externally corky brown or mottled, the walls 8–20 mm thick, the orifice broad, subentire, comprising ¾ or more of the total width of the receptacle, the internal receptacle surface corky brown, with numerous short, bluntly columnar 4–6-sided styles 0.5–1 mm diam. by 0.5 mm long, often subtended by clusters of hairs, the pedicel and peduncle stout, 10–25 mm long by 6–20 mm diam. Mature carpels ovoid-compressed, 9–13 mm long, 4–8 mm wide, 3–6 mm thick, the endocarp dark brown, lustrous, the surface scrobiculate. Gametic chromosome number, $n = 19$.

Distribution. Endemic to Mauritius (Fig. 40).

Habitat. The commonest and most widely distributed species of *Tambourissa* in Mauritius, *T. peltata* displays a wide ecological amplitude, ranging from lowland wet forest (e.g., at Bel Ombre, ca. 300 m, annual precipitation 2,400 mm), to upland evergreen moist forest (e.g., Mt. Corps de Garde, 750 m, annual precipitation 1,600 mm), or cloud forest (e.g., Mt. Cocotte, 760 m, annual precipitation 5,000 mm). Locally abundant in some areas, it may become a subcanopy or canopy tree (e.g., at Macabé high forest), or remain a stunted treelet (e.g., at Pétrin in *Philippia* heath formation).

MAURITIUS. BAMBOU MOUNTAIN RANGE: crest between Mt. Camisard and Piton Bambou, 28 July 1971 (fl), *Guého sub MAU 15052* (MAU). BASSIN BLANC CRATER: rain forest with *Calophyllum*, 550 m, 21 Dec. 1978 (st), *Lorence 2187* (MO). BEL OMBRE: June 1977 (fl), *Friedmann 3151* (P); wet forest with Sapotaceae, ca. 200–400 m, 27 Dec. 1978 (st), *Lorence 2213* (MO); (st), *Lorence 2214* (MO). BRISE FER MT.: Nov. 1960 (fr), *Lalouette 3008 sub MAU 10003* (*carpol. coll. 101*) (MAU). BELLE RIVE: (fr), *H. Rouillard s.n.* (MAU). CASCADE ALEXANDRA: S edge of central plateau, low, stunted wet forest, ca. 650 m, 25 Mar. 1979 (fl), *Lorence 2552* (MO). CHAMAREL HILL: top of hill, 1,100 ft. (ca. 350 m), 31 Jan. 1940 (fr), *Vaughan sub MAU 1912* (MAU, 2 sheets). CORPS DE GARDE MT.: summit ridge, ± stunted forest, ca. 750 m, 15 Nov. 1973 (fr), *Coode et al. 4064* (K, MAU). CROWN LAND RIVIÈRE: on bank along pipe to water tower, 30 July 1964 (fr), *Vaughan sub MAU 11009* (MAU). CUREPIPE: Forestry Department nursery, along stream bank with remnants of indigenous trees, ca. 700 m, 15 Dec. 1978 (fr), *Lorence 2151* (MAU, MO); 14 Mar. 1971 (fr), *Remy sub MAU 15489* (MAU). GAULETTES SERRÉES: north-central Mauritius, low mixed wet forest over lava, ca. 400–450 m, 19 May 1979 (fl), *Lorence et al. 2642* (K, MO); (fl, fr), *Lorence et al. 2643* (K, MO, P). LION MT.: by side of path leading to summit, along crest, 22 Mar. 1976 (fr), *Lalouette sub MAU 17878* (MAU). MACABÉ FOREST: Macabé to Brise Fer road, low mixed evergreen forest over laterite, ca. 660 m, 8 Dec. 1978 (fr), *Lorence 2101* (MAU, MO); Macabé forest, near kiosk, transitional wet forest, ca. 660 m, 16 Dec. 1978 (st), *Lorence 2154* (MO); Macabé forest, ca. 700 m, 7 Feb. 1975 (fr), *Lorence sub Coode 4791* (K, MAU); near path leading to Macabé via the marshes, 14 Feb. 1963 (fr), *Vaughan sub MAU 10682* (MAU, 2 sheets). MARE LONGUE PLATEAU: Mare Longue-Macabé road, on right bank of river flowing into Mare Longue reservoir, 10 Mar. 1967 (fl), *Guého sub MAU 12543* (MAU, 2 sheets); low, mixed wet forest along stream, ca. 700 m, 10 Apr. 1979 (fl), *Lorence 2586* (K, MAU, MO); 14 Apr. 1979 (fl), *Lorence 2593* (MO); near new reservoir, 1,900 ft. (ca. 600 m), 11 May 1946 (fr), *Vaughan V 3139* (*carpol. coll. 6*) (MAU, 2 sheets). MONTAGNE DES CRÉOLES: E Mauritius, transitional evergreen forest, ca. 250–300 m, 25 Jan. 1979 (st), *Lorence & Julien 2338* (MAU, MO); (fr), *Lorence & Julien 2339* (MAU, MO); (fr), *Lorence & Julien 2340* (MO); (fr), *Lorence & Julien 2341* (MO, P). PERRIER NATURE RESERVE: near Mare aux Vacoas, low mixed wet forest, ca. 600 m, 27 Mar. 1979 (fl), *Lorence 2555* (MO); 9 Apr. 1979 (fl), *Lorence 2585* (K, MO); 23 Apr. 1976 (fr), *Richardson et al. 4009* (K, MAU); (fr), *Richardson et al. 4010* (K); near quadrat by small stream, Dec. 1937 (fl), *Vaughan sub MAU 1437* (MAU, 2 sheets); (fl), *Vaughan sub MAU 1438* (MAU); 15 June 1939 (fl), *Vaughan sub MAU 1534* (MAU); 6 June 1969 (fl), *Vaughan sub MAU 13774* (MAU, 2 sheets); in dense indigenous thicket, 14 May 1970 (fl), *Vaughan sub MAU 14184* (MAU); (fl), *Vaughan sub MAU 14185* (MAU, 2 sheets); 22 Apr. 1970 (fl), *Vaughan sub MAU 14193* (MAU, 2 sheets); by stream, 9 Oct. 1975 (fr), *Vaughan sub MAU 17543* (MAU). PÉTRIN NATURE RESERVE: *Philippia* heath formation over laterite, 630 m, 4 Apr. 1979 (fl), *Lorence 2572* (MO, P). PIETER BOTH MT.: S flank below La Fenêtre, very degraded wet forest invaded by exotics, ca. 400 m, 23 Jan. 1979 (st), *Lorence 2319* (MAU, MO). PLAINE CHAMPAGNE: road to Plaine Champagne, dense indigenous thicket, 21 July 1966 (fr), *Guého sub MAU 12232* (MAU, 2 sheets); SE of triangulation point, low heath formation of *Philippia* and *Helichrysum* over laterite, ca. 700 m (fr), *Lorence 2197* (MAU, MO). POUCE MT.: Le Pouce Mt. plateau, mixed wet forest invaded by exotics, grading into cloud forest near summit, 600–700 m, 14 Dec. 1978 (fr), *Lorence 2146* (K, MO); 14 Feb. 1979 (fr), *Lorence 2402* (B, K, MAU, MO, P, REU, Z). SEPT CASCADES: (fr), *Hardy s.n.* (MAU). TAMARIN RIVER: river reserves near Tamarin River Bridge, at Mare aux Vacoas, 2 June 1966 (fl), *Vaughan sub MAU 12168* (MAU, 2 sheets); 5 May 1966 (fl), *Vaughan sub MAU 12240* (MAU, 2 sheets). VACOAS RIDGES: 21 Jan. 1968 (fr), *Guého sub MAU 13077* (*carpol. coll. 175*) (MAU). WITHOUT PRECISE LOCALITY: (fr), *Anon. sub MAU 11004* (*carpol. coll. 159*) (MAU); (fl), *Anon. 3132* (G); (st), *Bojer sub MAU 1312* (MAU); (fl), *Carmichael s.n.* (K, syntype); (st), *Carmichael s.n.* (K); (fr), *Remy s.n.* (MAU); 16 Aug. 1962 (fr), *Tilbrook sub MAU 10548* (MAU); 3 Sept. 1962 (fr), *d'Unienville sub MAU 10624* (MAU); 30 Mar. 1964 (fl), *d'Unienville sub MAU 11206* (MAU, 2 sheets).

Leaf shape in *Tambourissa peltata* is relatively variable, a character which tends to remain constant within populations. Populations from the eastern mountain ranges (e.g., Montagne des Créoles, Mt. de Lion, and Mt. Bambous) are characterized by narrowly elliptic to oblanceolate leaves, whereas most populations from the upland plateau have the usual obovate leaves. Fruit morphology ranges from typically cupuliform to flat and discoid, both extremes occasionally on the same tree (e.g., *Lorence 2151*). Androecious flower size and color are variable within populations but remain constant on a given tree. Dark purple-red androecious flowers are most common, whereas the salmon pink ones are less frequent. Gynoecious flower color is less variable, the central disc being reddish orange and the sterile lobes dull purple-red and verrucose. At anthesis, the disc secretes a copious thick, clear mucilage which covers the styles and is probably functional in pollination (see Endress, 1979, 1980b). Flowers of both sexes produce strong, sour odors of fermenting fruit or tomatoes.

Tambourissa peltata belongs to the small species Group 9, whose members are characterized by ternate to subalternate leaves, also including *T. ficus* (Mauritius) and *T. castri-delphinii* (Madagascar). *Tambourissa peltata* strongly resembles and is apparently closely related to the latter species; both are ramiflorous with similar androecious flowers and stamens, and have leaves with prominent, finely reticulate venation. *Tambourissa peltata* differs by its larger, solitary or fasciculate androecious flowers and is the only species known to have flat, discoid gynoecious flowers with star-like sterile lobes. Flowers of *T. ficus* are much larger than those of the preceding species and are produced at the swollen base of the trunk. The only other dioecious species in Mauritius, *T. cordifolia,* does not seem to be closely related to *T. peltata,* but rather belongs to species Group 5, although the two are known to hybridize naturally at Pétrin.

Vernacular name. Bois tambour (Mauritius).

IMPERFECTLY KNOWN SPECIES

39. Tambourissa lastelliana (Baill.) Drake in Grandidier, Hist. Phys. Madagascar 1(1): 24. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 44. 1911. *Monimia lastelliana* Baill., Bull. Mens. Soc. Linn. Paris 1: 342. 1882; Perk. & Gilg, Pflanzenr. 4, 101: 65. 1901. TYPE: Madagascar. Without precise locality, 1841, *de Lastelle s.n.* (holotype, P).

Dioecious (?) shrub or tree (?), the mature leafy stem glabrous, 4 mm diam., longitudinally striate-pustular, the rays relatively narrow, the nodes dilated, with multiple axillary buds, the internode 80 mm long. Leaves opposite, petiolate; petiole recurved, 15 mm by 2 mm, glabrescent; lamina thickly chartaceous, brown, adaxially glabrescent, abaxially with scattered simple, straight to slightly curved simple hairs 0.5 mm long, denser and longer (to 1–1.5 mm) along the major veins and costa, the lamina broadly obovate-cuneate, ± involute, the apex shortly acuminate, the base cuneate, the apical portion of the lamina with 4–5 pairs of broad, deltoid teeth 1.5–4 mm long, the tips indurated, the venation mixed, basally festooned brochidodromous, apically craspedodromous, the secondary veins excurrent into the marginal teeth, ca. 5 pairs, making a 35–40° angle with the costa, the venation strongly depressed adaxially and visible to 3°, raised abaxially and visible to 4°, the margin revolute. Androecious inflorescence ramiflorous (?), presumably a dichasium or the flowers solitary, the floral axis pilose-tomentose basally, fulvous, ca. 10 mm by 1.5 mm or longer, subtended by several obtuse-deltoid tomentose bracteoles. Submature androecious flower in bud 6–7 mm diam., globose, densely golden pilose externally, the apex slightly depressed, with several minute tepals, the pedicel ca. 5 mm by 1 mm, golden pilose; stamens ca. 60–70 per flower, in bud ca. 3–4 mm long by 1 mm wide, the loculi lateral, separate, occupying the medial ⅔ of the stamen, laterally dehiscent, the filament short, the connective prolonged, acute, the internal receptacle surface with scattered simple hairs between the stamens; tanniferous idioblasts and oil cells present in the receptacle wall.

Distribution. Presumably endemic to Madagascar. The type is said to be from eastern Madagascar (Baillon, 1882), presumably from low or mid altitude evergreen wet forest.

The type of *Monimia lastelliana* consists of a single, detached leaf, a leafless twig, and several detached androecious flower buds. Unlike *Monimia,* which has entire leaves with festooned brochidodromous venation and predominantly or uniquely stellate trichomes, the leaf of *de Lastelle s.n.* has dentate margins in the apical portion, mixed craspedodromous and brochidodromous venation, and bears only simple trichomes as do the flower buds. Furthermore, stamens of *de Lastelle s.n.* lack the paired basal appendages characteristic of *Monimia* and have instead long, laterally dehiscent loculi and an acutely prolonged connective, all lacking in *Monimia* as noted by Perkins (1911). The pollen is too immature to permit diagnosis. Nevertheless, it is clear that *de Lastelle s.n.* does not represent a species of *Monimia,* nor even belong in the subfamily Monimioideae (sensu Thorne, 1974), and was correctly removed from the genus by Drake del Castillo (1902).

Its eglandular stamens with laterally dehiscent loculi, and long, uniquely simple trichomes instead suggest placement in the subfamily Mollinedioideae (sensu Thorne, 1974) with the other Madagascan genera. The globose buds with minute, reduced tepals most closely recall those of

Tambourissa. Although venation is festooned brochidodromous in most *Tambourissa* species, that of *T. longicarpa* and *T. thouvenotii* is basally brochidodromous and tends to become craspedodromous in the toothed apical portion of the lamina, much as in *de Lastelle s.n.* On the basis of androecious floral morphology and leaf structure, it is most probable that *de Lastelle s.n.* actually does represent a species of *Tambourissa* as proposed by Drake del Castillo (1902).

40. Tambourissa sp. A.

Habit unknown. Leaves opposite, petiolate; petiole 17–24 mm long; lamina chartaceous, elliptic, 80–100 mm by 34–43 mm, the apex acuminate, the base cuneate, the venation visible to 5–6° on both surfaces. Androecious inflorescence (cauliflorous?) a dichasium, the elongate floral axis ca. 130 mm long; the androecious flower in bud cylindrical, obovoid-ellipsoid, ca. 12–15 mm long, apiculate, the pedicel 7 mm by 1 mm; at anthesis splitting deeply into 3 segments; stamens numerous, ligulate, ca. 2 mm long, the loculi confluent apically, occupying nearly the entire length of the stamen; flowers red when living. Gynoecious flowers, gynoecious inflorescence, and fruit unknown.

MADAGASCAR. TAMATAVE: Iaroka, Maroantsetra, 1,000 m, 20 June 1968 (fl), *Rakotozafy 847 bis* (MAD).

The elongate androecious buds most closely resemble those of *Tambourissa quadrifida* from Mauritius. It probably represents an undescribed species from the mid altitude *Tambourissa/Weinmannia* wet forest zone.

41. Tambourissa sp. B.

These collections have opposite leaves, the petiole to 23 mm long; lamina coriaceous, obovate, to 85 mm by 48 mm, the apex obtuse, emarginate, the base cuneate, the margin revolute. Immature androecious flower buds ramiflorous on leafless nodes, solitary, the pedicel ca. 20 mm long, the bud 7–8 mm diam., the stamens with lateral loculi and a prolonged connective.

MADAGASCAR. FIANARANTSOA: Ampamaherana, 14 Dec. 1949 (fl), *Anon. sub SF-1252* (MAD, P).

The species resembles *Tambourissa crassa* from Réunion in leaf, but in the latter species the flowers are larger and always terminal, and the connectives are not prolonged. This collection probably represents an undescribed species for which I could not find the precise locality on any map.

42. Tambourissa sp. C.

Tambourissa amplifolia sensu Cavaco in Humbert, Fl. Madagascar 80: 34. 1959 non (Bojer ex Tul.) A.DC.

Tree to 5 m, the leaves large, the petiole 10–16 mm long, the lamina ovate-elliptic, 140–180 mm by 60–80 mm, shortly acuminate apically, rounded basally, the secondary veins 4–7 pairs. Unlike *Tambourissa amplifolia* (Mauritius), the petioles, costa, and veins are densely hirtellous abaxially.

MADAGASCAR. FIANARANTSOA: Farafangana, Befotaka, 17 Aug. 1926 (st), *Decary 5040* (MAD, P); NE Madagascar, without precise locality (st), *Thiny s.n. in 1904* (P).

These collections either represent an undescribed species from the lowland wet forest zone in the northeast and east, or may be referable to *T. decaryana,* for which only inflorescence leaves are known.

43. Tambourissa sp. D.

Habit unknown. Leafy stems pale brown, velutinous, 1.5–2 mm diam., the new growth velutinous. Leaves opposite, petiolate; petioles 5–10 mm by 1 mm, velutinous; lamina subcoriaceous, adaxially glabrescent, abaxially pubescent, especially along the costa and major veins, ovate-elliptic, the apex acute to shortly acuminate, the base acutely cuneate, slightly decurrent, the secondary veins 4–6 pairs, making a 55–60° angle with the costa, the venation visible to 2(–3°) adaxially, to 4° abaxially, the margin entire, revolute. Flowers unknown. Fruiting receptacle (fide Baron's pencil sketch of *6720,* K) terminal, subglobose, ca. 45–55 mm diam., the orifice subcircular, subentire, comprising ca. ¼–⅓ total width of the fruit. Mature carpels unknown.

MADAGASCAR. N Madagascar (probably DIEGO SUAREZ): without precise locality, ca. 1882 (st), *Baron 6720* (K; see also Baron's sketch of a fruit with the specimen).

Distribution. Presumably endemic to Madagascar.

The collection consists of two sterile leafy branches plus Baron's pencil sketch of the fruit. The leaves are similar to those of *Tambourissa sieberi* (Mauritius), but differ in having numerous oil cells dispersed throughout the laminar tissue and in having less highly branched venation (only to 4°), nor does *T. sieberi* ever have solitary, terminal fruits. It probably represents an undescribed species.

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